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FLORAL BIOLOGY OF *BABIANA*
(IRIDACEAE: CROCOIDEAE):
ADAPTIVE FLORAL RADIATION
AND POLLINATION¹

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ABSTRACT

Field observations, floral dissections, floral nectar, and pollen load analyses of captured insects of 53 species of *Babiana* Ker Gawl. show that flowers of this geophytic genus of some 90 species of Iridaceae subfamily Crocoideae, predominantly of the southern African winter-rainfall zone, are cross pollinated by a wide range of animals. These include passerine birds and insects of four different orders, Hymenoptera (mainly Apidae), Diptera (mainly Nemestrinidae), Coleoptera (Scarabaeidae), and Lepidoptera (mainly Noctuidae). Apid pollination involves two discrete systems—passive pollination by anthophorines and native *Apis mellifera* foraging for nectar and active pollen gathering by *A. mellifera* and other Apoidea foraging for pollen. From what is known about relationships within *Babiana* and Crocoideae, it seems likely that passive pollination by anthophorines and honeybees, with nectar secreted in zygomorphic, bilabiate flowers as a reward, is the ancestral condition; it is also the most common, demonstrated for 18 and inferred for 35 more species from all three taxonomic sections of the genus. Active pollination by honeybees and female Apoidea foraging for pollen was demonstrated in one species and is inferred for four more, all of which have radially symmetric flowers and prominent anthers. Pollination by long-proboscid nemestrinids, mostly species of *Prosoeca*, is recorded for 13 species and inferred for five more, while moth pollination is recorded for one species and inferred for another two. Pollination exclusively by hopline scarab beetles, known for six species, is associated with development of radial symmetry of the flower. Passerine bird pollination, associated with the classic syndrome of a wide floral tube, red floral pigmentation, and rigid, well-exserted stamens, occurs in two species, and is inferred for one more. Species with a bimodal system in which bees and beetles both visit and accomplish pollen transfer is known for three species. Comparing pollination systems with what is known about species relationships in *Babiana*, we infer that long-proboscid fly pollination evolved at least four times and moth pollination three times. Active pollination by pollen-collecting bees and hopline beetle pollination also probably evolved three times each and bird pollination twice. Pollination systems are labile, and we postulate that there has been a minimum of 14 shifts in pollination system, approximately one shift for every six species. Lastly, *Babiana* species show the same correlation of morphology and floral presentation with particular sets of pollinators, described for several other genera of Iridaceae, e.g., *Gladiolus* L., *Hesperantha* Ker Gawl., and *Lapeirousia* Pourr., as well as Geraniaceae and Orchidaceae. This increases our confidence in predicting pollinators on the basis of floral presentation in other species and genera in which pollinators have not been established.

Key words: *Babiana*, Crocoideae, Iridaceae, pollination, southern Africa, winter-rainfall zone.

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Studies of the pollination ecology of the African Iridaceae have repeatedly shown that medium-sized to large genera exhibit an unusual degree of plasticity in floral morphology and that, consequently, species of each genus are pollinated by different sets of insect or avian pollinators. Moreover, the speciation and radiation of these genera are closely associated with shifts in their pollinators (Bernhardt & Goldblatt, 2000; Goldblatt et al., 2001). For example, different species of *Lapeirousia* Pourr. are pollinated by long-proboscid flies, nectar-feeding bees, or moths, or, in a few instances, a mix of bees, bee-flies, and butterflies (Goldblatt et al., 1995). The majority of species of *Gladiolus* L. appear to be pollinated primarily by nectar-feeding anthophorine bees (Goldblatt et al., 1998a), but some red-flowered species are pollinated by the large satyrid butterfly, *Aeropetes* (Johnson & Bond, 1994; Goldblatt & Manning, 2002); others are dependent on pollen-collecting female andrenid and halictid bees (or a combination of these bees and hopliine beetles) (Goldblatt et al., 1998b), long-proboscid flies, moths, or birds (Goldblatt & Manning, 1999, 2002; Goldblatt et al., 1999). Consequently, adaptive radiation of pollination-related floral characters appears to have played a prominent role in evolution and speciation within African Iridaceae.

The southern African genus *Babiana* Ker Gawl., with some 90 species of corm-bearing geophytes (Goldblatt & Manning, 2007 and unpublished data), is one of the few remaining larger genera of southern African Iridaceae for which data on pollination ecology are deficient. Floral variation in the genus is, however, extensive, and we undertook this study of the pollination ecology of *Babiana* to determine to what extent pollination mechanisms correlate with floral morphology and phylogeny. *Babiana* is exceptional in subfamily Crocoideae in the dominance of blue flowers among the species. In addition, it has radiated most extensively in the arid, winter-rainfall semi-desert areas of western southern Africa that surround the Cape Floristic Region.

METHODS

INFLORESCENCE PHENOLOGY AND FLORAL LIFE SPAN

Direct observations are presented on 54 taxa of *Babiana* (53 species and one subspecies) made in the field from 1993 to 2004 (Table 1) across the entire geographic range of the genus. Supplementary observations were made on living collections at Kirstenbosch Botanic Gardens, Cape Town, South Africa, and in Portland, Oregon, U.S.A. The taxonomy followed is that of Goldblatt and Manning (2007). Field observations were made in the southern winter

and spring at sites in southern Africa, in the Northern and Western Cape Provinces of South Africa, which have a Mediterranean-type climate with wet winters and dry summers. Observations of insect foraging involved 4–10 hours per plant species and included recording of floral attractants (pigmentation, scent), rewards (nectar, pollen), the mode and timing of anthesis (opening of individual buds), daily phenology, anther dehiscence, expansion of stigmatic lobes, the behavior of insects on the flower, and the taxonomic diversity of floral foragers. Floral scent was noted in the field and in cultivated plants. Scents too weak to be detected by the human nose were recorded after individual flowers were picked and placed in clean, lidded glass jars and stored in a warm place. The contents of each jar were smelled after a minimum of 60 minutes (Buchmann, 1983).

Flower longevity estimates were made using greenhouse-cultivated plants. Flowers were identified with dated jeweler's tags on the day they opened and were monitored daily until the perianth collapsed, at which point the tag was again dated and then removed.

NECTAR ANALYSIS

Standing crop nectar volume measurements were taken primarily from unbagged flowers in the field and reflect both rates of secretion and depletion. Nectar volume is expected to be lower in unbagged versus bagged flowers, but sampling of nectar of unbagged flowers in populations being visited by pollinators reflects a realistic situation that confronts a pollinator in the field. To collect nectar, whole flowers were picked, and nectar was withdrawn from the base of the perianth tube with 3- μ l capillary tubes after separating the ovary from the perianth base. The percentage of sucrose equivalents in fresh nectar was measured in the field using a Bellingham and Stanley (Tunbridge Wells, United Kingdom) handheld refractometer (0%–50%) from five or more individuals per population, unless fewer individuals were available. Additional nectar samples were dried on Whatman filter paper no. 1 (Whatman International Ltd., Springfield Mill, United Kingdom) and sent to B.-E. van Wyk, Rand Afrikaans University, Johannesburg, for high-performance liquid chromatography nectar chemistry analysis (van Wyk et al., 1993).

COMPATIBILITY RELATIONS

Compatibility relationships of *Babiana* species were examined in some greenhouse-cultivated plants using one to three genets each of eight species. Plants were isolated from insect foragers with nylon netting. Individual flower buds were tagged with jeweler's tags. For

one set of flowers, we self-pollinated the stigma by hand with the contents of dehiscent anthers from the same flower (autogamy) or flowers on the same inflorescence (geitonogamy). The pollinated flowers were then checked after 42 days (six weeks) to observe capsule production. For a second set of flowers, we kept plants isolated from insect foragers but did not hand-manipulate blooms in any way in order to determine whether mechanical self-pollination (autogamy) occurs in flowers in the absence of pollen vectors.

INSECT OBSERVATION AND POLLEN LOAD ANALYSES

Observations of insects on *Babiana* flowers included whether insects contacted anthers and stigmas while foraging. Only insects observed probing the floral tube or brushing the anthers or stigmas were captured and killed in a jar using ethyl acetate vapor. To prevent contamination of the body of an insect with pollen carried by another in the same jar, each insect was wrapped in tissue as soon as it was immobilized. Body and proboscis lengths were recorded from captured specimens. Capturing some insects (especially long-proboscid flies) at some sites appeared to reduce the population significantly, and we therefore killed as few insects as necessary to obtain specimens for identification and pollen load analysis. Removal of pollen from insect bodies after they were pinned involved gently scraping pollen off the body with a dissecting needle (see Goldblatt et al., 1998a, b). The residue from needle probes was collected on glass slides and mounted in one or two drops of Calberla's fluid (Ogden et al., 1974). In the case of long-proboscid flies, which are large insects, sites of pollen deposition are often quite discrete for a particular plant visited, and pollen species can usually be identified without recourse to microscopic examination due to pollen color and position. Pollen grains were identified microscopically by comparison with a reference set of pollen grain preparations made from plants flowering at study sites. *Babiana* pollen grains are recognized by their large size, perforate-scabrate exine, and monosulcate aperture with prominent 2-banded operculum (Goldblatt et al., 1991).

Insect specimens were identified by R. W. Brooks, University of Kansas (Apoidea); H. Dombrow, Worms, Germany (Scarabaeidae); and J. C. Manning (Diptera, Lepidoptera). Voucher specimens are deposited at the Snow Entomological Museum, Lawrence, Kansas.

RESULTS

INFLORESCENCE PHENOLOGY AND FLORAL LIFE SPAN

Babiana species are corm-bearing geophytes that have an erect or spreading inflorescence of sessile

flowers (a spike) arranged in a spiral, in two ranks, or in more or less a single rank (Figs. 1A, 2A). Exceptionally, the spike may reach to 1 m or more in *B. thunbergii* Ker Gawl., but lengths of 10–40 cm are more usual and several species have the flowers borne close to the ground with the spike reaching only shortly above the ground. Aerial stems may be simple or branched, sometimes repeatedly, and the lateral branches bear fewer flowers than the main axis. Flowering is closely synchronized within the same population and generally lasts two to four weeks. *Babiana ringens* (L.) Ker Gawl. is unique in having the thickened, sturdy main axis sterile, and the flowers are borne on a lateral branch close to ground level. The sterile axis functions as a perch for visiting sunbirds (Marloth, 1915; Goldblatt et al., 1999). Flowering periods in the genus subdivide into a winter season (May to July) or a spring season (August to early October) in the southern African winter-rainfall zone (Table 2); only *B. bainesii* Baker, not included in our study, flowers in late summer and autumn (February to April) in eastern southern Africa, which has a summer-rainfall climate with a cold, dry winter.

The pattern of anthesis on an inflorescence is acropetal. In all species, a mature bud expands in the early morning, and, in most species, the flowers close again in the late afternoon or at sunset. Exceptions are members of section *Antholyzoides*; the two bird-pollinated species, *Babiana ringens* and *B. thunbergii*; and the putatively moth-pollinated *B. noctiflora* Goldblatt & J. C. Manning, *B. patersoniae* L. Bolus, and *B. virginea* Goldblatt. In the two bird-pollinated species, as well as in *B. spathacea* (L. f.) Ker Gawl., the tepal orientation is apparently too complex for the flowers to close, whereas in the moth-pollinated species the flowers remain open to permit access to pollinators. A flower typically lasts three to five days under greenhouse conditions when not pollinated but maintains the pattern of opening and closing at specific times. We have no data on longevity in cross-pollinated flowers. Flower buds on the same inflorescence open sequentially, usually one to two days apart. On plants with branched stems, there may be several flowers open at any time. When flowers close, the tepals loosely cloak the anthers and stigmas. Ambient temperature influences anthesis and on cold (less than 15°C), overcast, or misty days, a flower may not open at all, or the normal timing of opening may be delayed until conditions are favorable.

Flowers of all species studied are protandrous. The anthers dehisce longitudinally within one to four hours after the tepals first unfold. This depends to some extent on ambient temperature and humidity (see above), and anthers dehisce later in the day under wet-cool conditions. The style divides into three

Table 1. Study sites and voucher information for *Babiana* species studied. Vouchers are housed at MO (Goldblatt, Goldblatt & Manning) or at NBG (all collectors) unless indicated to the contrary. All study sites are in South Africa.

Species	Study site	Voucher
<i>B. ambigua</i> (Roem. & Schult.) G. J. Lewis	Western Cape, Mamre Veld Reserve	<i>Goldblatt & Porter 11878</i>
<i>B. angustifolia</i> Sweet		
site 1	Western Cape, Versfeld Reserve, Darling	<i>Goldblatt & Manning s.n.</i> , no voucher
site 2	Western Cape, Elandsberg Farm, Gouda	<i>Goldblatt 11221</i>
<i>B. attenuata</i> G. J. Lewis	Northern Cape, near Gargams	<i>Goldblatt & Manning 11323</i>
<i>B. brachystachys</i> (Baker) G. J. Lewis	Northern Cape, near Hondeklipbaai	<i>Goldblatt & Manning 9997</i>
<i>B. carminea</i> J. C. Manning & Goldblatt	Western Cape, Knersvlakte	<i>Goldblatt & Manning 10662</i>
<i>B. cedarbergensis</i> G. J. Lewis	Western Cape, Cedarberg Mtns.	<i>Goldblatt & Porter 12165</i>
<i>B. crispa</i> G. J. Lewis	Northern Cape, Bidouw Hills	<i>Goldblatt & Manning 11077</i>
<i>B. cuneata</i> J. C. Manning & Goldblatt	Western Cape, Katbakkies Pass	<i>Goldblatt & Manning 11457</i>
<i>B. curviscapa</i> G. J. Lewis		
site 1	Northern Cape, Leliefontein	<i>Goldblatt & Manning 10007</i>
site 2	Northern Cape, Spektakel Pass	<i>Goldblatt & Manning 9970</i>
site 3	Northern Cape, S of Springbok	<i>Goldblatt & Manning 11326</i>
site 4	Northern Cape, Kamiesberg, farm Botuin	<i>Goldblatt & Porter 11903</i>
site 5	Northern Cape, Springbok	<i>Goldblatt & Porter 12087</i>
<i>B. dregei</i> Baker		
site 1	Northern Cape, Kamiesberg, farm Sneekop	<i>Goldblatt & Manning 9279</i>
site 2	Northern Cape, near Leliefontein	<i>Rodin 1145</i>
<i>B. ecklonii</i> Klatt		
site 1	Western Cape, Gilberg	<i>Goldblatt & Manning 10967</i>
site 2	Western Cape, Piekenienskloof Pass	<i>Goldblatt & Porter 12262</i>
<i>B. engysiphon</i> J. C. Manning & Goldblatt	Northern Cape, Moedverloor rd.	<i>Goldblatt & Porter 12137</i>
<i>B. fimbriata</i> (Klatt) Baker	Northern Cape, near Garies	<i>Goldblatt & Nänni 11152</i>
<i>B. flabellifolia</i> Klatt	Northern Cape, Anenous Pass	<i>Goldblatt & Manning 11367</i>
<i>B. fragrans</i> (Jacq.) Ker Gawl.		
site 1	Western Cape, Signal Hill, Cape Town	<i>Sidey 2186</i>
<i>B. framesii</i> L. Bolus		
site 1	Northern Cape, Nieuwoudtville Reserve	<i>Vordenstam 3012 (S)</i>
site 2	Northern Cape, Farm Glenlyon	<i>Nänni 159</i>
<i>B. geniculata</i> G. J. Lewis	Western Cape, Biedouw Valley	<i>Goldblatt & Manning 9923</i>
<i>B. inclinata</i> Goldblatt & J. C. Manning		
site 1	Western Cape, near Porterville	<i>Goldblatt & Manning 9363</i>
site 2	Western Cape, N of Piketberg	<i>Goldblatt & Manning 11932</i>
<i>B. latifolia</i> L. Bolus	Western Cape, N of Piketberg	<i>Goldblatt & Porter 12127</i>
<i>B. leipoldtii</i> G. J. Lewis	Western Cape, Mamre Rd.	<i>Goldblatt & Nänni 11089</i>
<i>B. lineolata</i> Klatt		
site 1	Western Cape, Cold Bokkeveld	<i>Goldblatt 11631</i>
<i>B. melanops</i> Goldblatt & J. C. Manning		
site 1	Western Cape, near Mamre	<i>Goldblatt & Nänni 11095</i>
site 2	Western Cape, Darling Hills	<i>Goldblatt & Nänni 11095A</i>
site 3	Western Cape, S of Tulbagh	<i>Goldblatt 11420</i>
<i>B. montana</i> G. J. Lewis	Western Cape, Fairfield	<i>Goldblatt & Nänni 10250A</i>
<i>B. mucronata</i> subsp. <i>mucronata</i> (Jacq.) Ker Gawl.		
site 1	Western Cape, Olifants River valley	<i>Goldblatt & Manning 10937</i>
site 2	Western Cape, Piekeniens Kloof	<i>Goldblatt & Manning 11674</i>
<i>B. nana</i> (Andr.) Spreng.	Western Cape, Mamre	<i>Goldblatt & Nänni 11549</i>
<i>B. noctiflora</i> Goldblatt & J. C. Manning	Western Cape, Paardeberg	<i>Goldblatt & Nänni 11172</i>
<i>B. odorata</i> L. Bolus		
site 1	Western Cape, near Malmesbury	<i>Goldblatt 2184</i>
site 2	Western Cape, near Hopefield	<i>Goldblatt & Manning 11418</i>
<i>B. papyracea</i> Goldblatt & J. C. Manning	Northern Cape, Nieuwoudtville	<i>Goldblatt 11609, 11617</i>
<i>B. patersoniae</i> L. Bolus	Western Cape, near Napier	<i>Goldblatt & Manning 9954</i>

Table 1. Continued.

Species	Study site	Voucher
<i>B. patula</i> N. E. Br.	Western Cape, near Worcester	Goldblatt 11091
<i>B. praemorsa</i> Goldblatt & J. C. Manning	Northern Cape, Hantamsberg	Goldblatt & Manning 9961
<i>B. pubescens</i> (Lam.) G. J. Lewis	Northern Cape, Garies hills	Goldblatt & Manning 9907
<i>B. purpurea</i> (Jacq.) Ker Gawl.	Western Cape, near Botrivier	Goldblatt 11112
<i>B. pygmaea</i> (Burm. f.) Baker	Western Cape, near Hopefield	Goldblatt & Manning 11415
<i>B. regia</i> (G. J. Lewis) Goldblatt & J. C. Manning	Western Cape, near Kraaifontein, Farm Joostenbergkloof	Goldblatt & Manning 11558
<i>B. rigidifolia</i> Goldblatt & J. C. Manning	Western Cape, Botterkloof Pass	Goldblatt & Manning 10523
<i>B. ringens</i> (L.) Ker Gawl.		
site 1	Western Cape, near Yzerfontein	Goldblatt s.n., no voucher
site 2	Western Cape, N of Aurora	Goldblatt s.n., no voucher
<i>B. rubrocyanea</i> (Jacq.) Ker Gawl.	Western Cape, Darling, Waylands	Goldblatt & Manning 11555
<i>B. sambucina</i> subsp. <i>sambucina</i> (Jacq.) Ker Gawl.		
site 1	Western Cape, near Touwsrivier	Goldblatt & Nänni 11465
site 2	Western Cape, near Barrydale	Goldblatt & Manning 9991
site 3	Western Cape, near Ladismith	Goldblatt & Porter 12184
site 4	Western Cape, Kammanassie foothills	Goldblatt & Porter 12289
site 5	Western Cape, Cango valley	Goldblatt & Porter 11838
subsp. <i>longibracteata</i> G. J. Lewis	Northern Cape, near Nieuwoudtville	Goldblatt & Manning 9973
<i>B. scabrifolia</i> Brehm ex Klatt		
site 1	Western Cape, Olifants River valley	Goldblatt & Manning 11081
site 2	Western Cape, near Trawal	Goldblatt & Manning 11445
<i>B. scariosa</i> G. J. Lewis		
site 1	Northern Cape, S of Nieuwoudtville	Goldblatt 11609
site 2	Western Cape, Kobbie valley	Goldblatt 11614
<i>B. sinuata</i> G. J. Lewis	Western Cape, near Bullshoek	Goldblatt 11443
<i>B. spathacea</i> (L. f.) Ker Gawl.		
site 1 (cream flowers)	Northern Cape, 19 km S of Nieuwoudtville	Goldblatt & Manning 10033
site 2 (lilac flowers)	Northern Cape, 8 km S of Nieuwoudtville	Goldblatt & Manning 10034
<i>B. spiralis</i> Baker	Northern Cape, Garies hills	Goldblatt & Nänni 11453
<i>B. stricta</i> (Aiton) Ker Gawl.		
site 1	Western Cape, Brandvlei hills	Goldblatt & Manning 11129; Goldblatt & Porter 12172A
site 2	Western Cape, near Swellendam	Goldblatt 11434
<i>B. thunbergii</i> Ker Gawl.	Western Cape, Lambert's Bay	Hall 4539
<i>B. tritonioides</i> G. J. Lewis	Northern Cape, Komaggas	Goldblatt & Porter 12095
<i>B. tubiflora</i> (Burm. f.) Ker Gawl.		
site 1	Western Cape, Rondebeg	Goldblatt s.n., no voucher
site 2	Western Cape, Ganzekraal	Goldblatt & Manning s.n., no voucher
<i>B. unguiculata</i> G. J. Lewis	Northern Cape, S of Nieuwoudtville	Goldblatt & Porter 12431
<i>B. vanzijliae</i> L. Bolus		
site 1	Northern Cape, Matjesfontein, S of Nieuwoudtville	Goldblatt & Nänni 11107
site 2	Northern Cape, Blompad, Nieuwoudtville	Goldblatt & Nänni 11401
<i>B. villosa</i> (Aiton) Ker Gawl.		
site 1	Western Cape, near Tulbagh	Goldblatt & Porter 11426A
site 2	Western Cape, Malmesbury	Goldblatt 11424
<i>B. villosula</i> (J. F. Gmel.) Ker Gawl. ex Steud.		
site 1	Western Cape, Mamre Rd.	Goldblatt 11088
site 2	Western Cape, Potsdam	Manning s.n., no voucher
site 3	Western Cape, Silvermine	Goldblatt 11312
<i>B. virginea</i> Goldblatt	Northern Cape, near Ganagga Pass	Goldblatt & Manning 10746

Table 2. Floral characteristics of *Babiana* species arranged according to flower type. Features are for populations studied and may not reflect the variation in the entire species. Measurements of the perianth tube were taken from the base of the tube to the point at which the tepals separate. + = presence of small quantities; ++ = moderate to large quantities of nectar; tr = trace amount too little to measure volumetrically. Flower shapes follow the terminology of Faegri and van der Pijl (1979).

Species	Flower shape	Flower color	Tube, mm	Scent	Nectar	Flowering time
<i>B. ambigua</i> group (pollinated by large-bodied anthophorine bees)						
<i>B. ambigua</i>	gullet	bluish with white	10–19	musky	++	Aug.–Sept.
<i>B. attenuata</i>	gullet	bluish with white	25–35	violet	++	Aug.
<i>B. cedarbergensis</i>	tube-gullet	blue-violet with white	16–18	light violet	++	Sept.
<i>B. crispa</i>	gullet	pale blue with white	14–20	musky	+	July–Aug.
<i>B. cuneata</i>	tube-salver	blue-violet with white	40–45	none	++	Aug.–Sept.
<i>B. fimbriata</i>	gullet	red-purple with yellow	10–12	sweet-clove	+	Aug.–Sept.
<i>B. flabellifolia</i>	gullet	blue or lilac with white	12–35	violet	+	July–Aug.
<i>B. fragrans</i>	gullet	violet or yellow with white	18–20	violet-clove	+	Aug.–Sept.
<i>B. inclinata</i>	gullet	blue with white	ca. 10	none	+	Sept.–Oct.
<i>B. lineolata</i>	gullet	blue with white	8–15	none	+	Sept.
<i>B. montana</i>	gullet	blue-mauve with white	15–20	light spicy	++	Aug.–Sept.
<i>B. mucronata</i>	gullet	blue-mauve with white	15–28	cinnamon-vanilla or musk	++	Aug.–Sept.
<i>B. nana</i>	gullet	bluish or pink with white	12–17	violet-rose	++	Aug.–Sept.
<i>B. odorata</i>	gullet	pale and deep yellow	10–14	violet, spice, and acid musk	++	July–Aug.
<i>B. patula</i>	gullet	mauve and yellow	10–14	violet-rose	++	July–Aug.
<i>B. purpurea</i>	salver	pink to mauve, anthers blue- black	18–28	light rose	+	Aug.–Sept.
<i>B. sambucina</i>	salver	blue with white	35–60	strong violet	++	Aug.–Sept.
<i>B. scabrifolia</i>	gullet	blue with white	12–18	Narcissus	+	July–Aug.
<i>B. scariosa</i>	gullet	lilac-mauve with blue	12–20	none	++	Sept.
<i>B. sinuata</i>	gullet	blue with yellow	8–9	light spicy	+	Sept.
<i>B. spiralis</i>	gullet	blue or mauve-pink with yellow	8–10	sweet-vanilla	+	Aug.–Sept.
<i>B. tritonioides</i>	gullet	mauve with yellow	6–8	violet	+	Aug.
<i>B. unguiculata</i>	gullet	pale yellow with white	10–12	light spicy	+	Aug.–Sept.
<i>B. villosula</i> group (pollinated by pollen-collecting female bees)						
<i>B. leipoldtii</i>	salver	blue, dark center, anthers white	15–20	light violet or acid musk	+	Aug.
<i>B. villosula</i>	bowl-salver	blue-mauve, white center, anthers blue to mauve	18–30	musky-violet	tr	July–Aug.
<i>B. framesii</i> group (pollinated by long-proboscid flies)						
<i>B. brachystachys</i>	tube-salver	pink with red	70–75	none	++	Sept.–Oct.
<i>B. curviscapa</i>	tube-gullet	blue-violet or magenta with white	36–43	none (magenta flowers) or light rose	++	Aug.–Sept.
<i>B. dregei</i>	tube-gullet	blue-violet with white	50–65	light rose	++	mainly Aug.
<i>B. ecklonii</i>	tube-gullet	violet with white	35–45	none	++	Sept.
<i>B. engysiphon</i>	tube-gullet	violet with white	35–47	none	++	Aug.–Sept.
<i>B. framesii</i>	tube-gullet	blue-purple with white	60–70	light violet	++	Aug.–Sept.
<i>B. geniculata</i>	tube-gullet	blue-purple with white	35–45	none	++	Aug.–Sept.
<i>B. latifolia</i>	tube-gullet	violet with white	30–40	none	++	Sept.
<i>B. praemorsa</i>	tube-salver	violet with white	40–60	none	++	Aug.–Sept.
<i>B. pubescens</i>	tube-gullet	blue-purple with white	ca. 50	none	++	Aug.–Sept.
<i>B. rigidifolia</i>	tube-gullet	violet with white	38–55	none	++	Sept.
<i>B. sambucina</i> subsp. <i>longibracteata</i>	tube-gullet	blue with white	40–55	violet or none	++	Aug.–Sept.
<i>B. spathacea</i>	tube-gullet	cream with red	35–45	none	++	Sept.–Oct.
<i>B. tubiflora</i>	tube-gullet	white with red	45–80	none	++	Aug.–Sept.

Table 2. Continued.

Species	Flower shape	Flower color	Tube, mm	Scent	Nectar	Flowering time
<i>B. tubulosa</i>	tube-gullet	white with red	65–90	none	++	Aug.–Sept.
<i>B. vanzijliae</i>	tube-gullet	yellow with cream	18–50	spicy musk	++	Aug.–Sept.
<i>B. pygmaea</i> group (pollinated partly or exclusively by hopliine beetles)						
<i>B. angustifolia</i>	bowl	deep violet, anthers black	10–17	none	tr	mainly Sept.
<i>B. melanops</i>	salver	pale to dark blue-mauve, darker center, anthers blue-violet to black	16–27	lemon-violet or none	+ or none	Aug.–Sept.
<i>B. papyracea</i>	salver	blue	35–45	none	none	Oct.
<i>B. pygmaea</i>	bowl	yellow, brown or purple center	15–25	none	none	Aug.–early Sept.
<i>B. regia</i>	bowl	dark blue, red center, anthers rust-brown	10–12	none	tr	Sept.–Oct.
<i>B. rubrocyanea</i>	bowl	dark blue, red center, anthers rust-brown	15–20	none	+	Aug.–Sept.
<i>B. stricta</i>	salver	white, mauve or pink, lower lateral tepals often white or yellow	10–18	faint rose	+	Aug.–Sept.
<i>B. villosa</i>	salver	deep red to magenta or pink, anthers black	12–17 or 30–36	none	none	Aug.–Sept.
<i>B. patersoniae</i> group (pollinated by moths)						
<i>B. noctiflora</i>	tube-gullet	cream, yellow markings	33–50	heavy sweet clove	++	Sept.
<i>B. patersoniae</i>	tube-gullet	cream flushed pink or blue	20–30	heavy sweet clove	++	Aug.–Oct.
<i>B. virginea</i>	tube-gullet	cream flushed mauve	60–65	heavy sweet clove	++	Sept.–Oct.
<i>B. ringens</i> group (pollinated by sunbirds)						
<i>B. carminea</i>	tube-gullet	red with yellow marks	56–60	none	++	July–Aug.
<i>B. ringens</i>	gullet	red, yellow throat	32–45	none	++	Aug.–Sept.
<i>B. thunbergii</i>	gullet	red	30–40	none	++	July–Aug.

slender branches at a point between the mouth of the perianth tube and the apex of the exerted anthers, depending on species. The style branches, the adaxial surfaces of which comprise the stigmatic surfaces, are held erect when the flower first opens but diverge later during the same day, spreading outward above or between the erect or divergent anthers. The stigmatic surfaces typically appear to become receptive on the second day of flowering, when the stigma lobes expand and then appear minutely hairy and glistening under a 10× hand lens.

Open flowers are either bilaterally symmetric (zygomorphic) and then held suberect or face to the side (Figs. 1, 2, 3C), or are radially symmetric and held erect or suberect with the tepals slightly cupped or spreading horizontally from the base (Fig. 3A, B). The stamens are symmetrically disposed in radially symmetric flowers or are unilateral and arcuate, lying below or in front of the dorsal tepal in zygomorphic flowers. The filaments are inserted just above the apex of the narrow part of the tube and are exerted a short distance. Anthers are developmentally extrorse with loculicidal dehiscence, and the pollen adheres to the dehisced anther locules. An unusual feature of a few

species of section *Babiana* is the sagittate anthers with an expanded connective, broadest at the base (Fig. 3B). The anthers and pollen in these species (e.g., *B. melanops* Goldblatt & J. C. Manning, *B. stricta* (Aiton) Ker Gawl., *B. villosa* (Aiton) Ker Gawl.) are darkly pigmented, either blackish or deep blue. In other species, the anthers and pollen are generally pale blue to whitish or rarely pale yellow.

FLORAL PRESENTATION AND POLLINATION SYSTEMS

Five main pollination systems can be recognized in *Babiana*, each characterized by a suite of morphological features including floral symmetry and orientation, tepal color, floral fragrance, and nectar quantity and concentration. Comparative floral traits of these systems are summarized in Table 2. The pollination systems and associated floral features are not always correlated with presumed natural relationships among the species, although these are still not completely understood (Goldblatt & Manning, 2007).

The Babiana ambigua group. In this group (Table 2), of which *Babiana ambigua* (Roem. & Schult.) G. J.

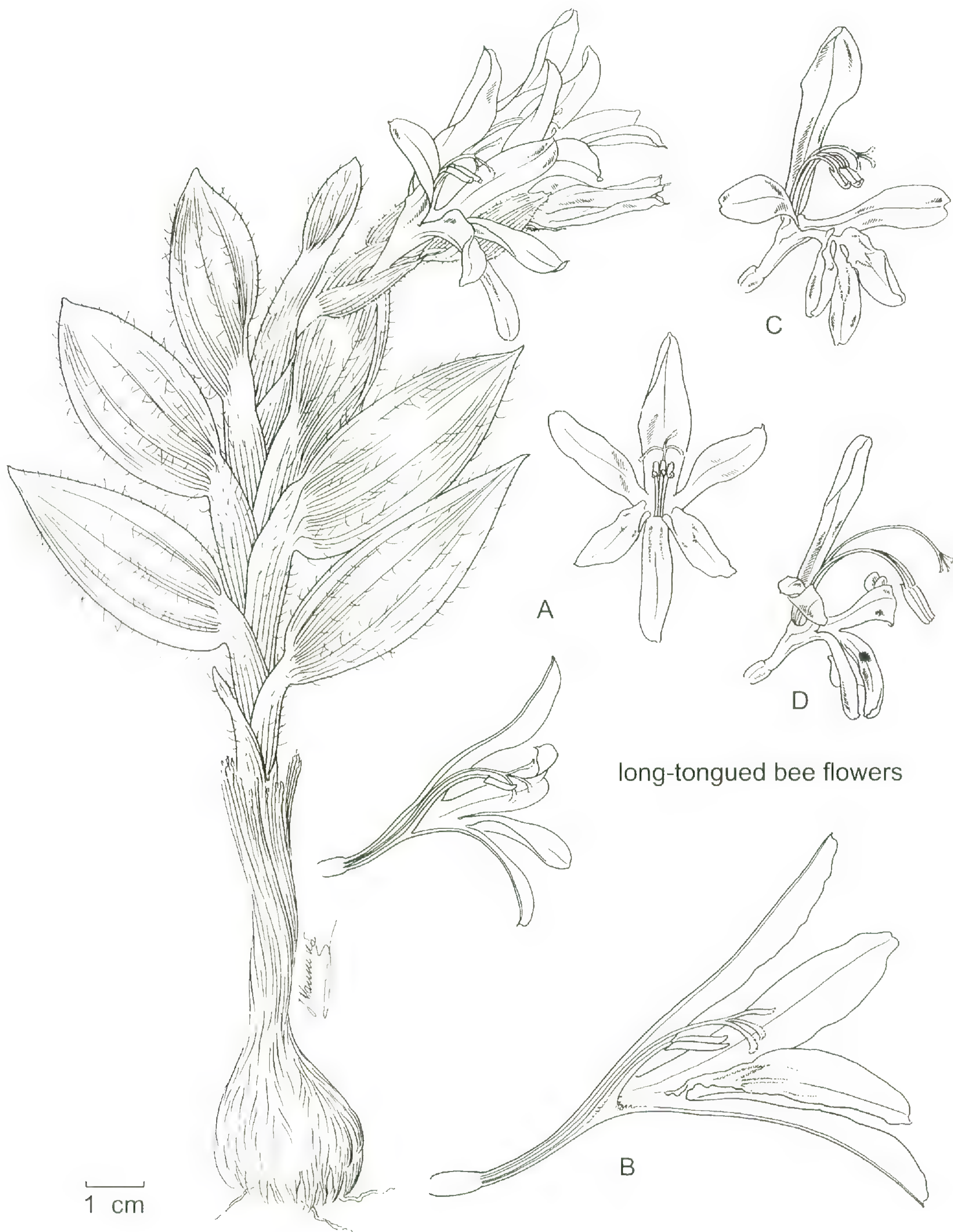


Figure 1. Flowers of *Babiana* species pollinated by large-bodied, long-tongued bees. —A. *Babiana rubella* (sect. *Teretifoliae*) with whole plant, and front and longitudinal section of flower. —B. *Babiana grandiflora* Goldblatt & J. C. Manning (sect. *Teretifoliae*), longitudinal section of flower. —C. *Babiana spiralis*, whole flower. —D. *Babiana sinuata* (both sect. *Exohebeoides*), whole flower; note strongly arched stamens and style. Drawn by John Manning from live plants. Scale bar = 1 cm; B, approximately 2× scale bar.

Lewis, *B. nana* (Andr.) Spreng., and *B. rubella* Goldblatt & J. C. Manning are typical examples, the flower is zygomorphic with a bilabiate perianth (Fig. 1A–D). Both style and stamens are unilateral and lie arched over the lower tepals, with the anthers

facing the landing platform formed by the lower three tepals and their adaxial (sterile) surface lying just below the dorsal tepal. The style lies arched above the unilateral stamens and divides opposite to slightly beyond the anther apices, while the style branches are

3–6 mm long and arch outward. The receptive ends of the style branches, which comprise the stigmas, are thus held distant from the anthers and pollen (i.e., herkogamy). Anthers and pollen are typically cream, pale yellow, or pale blue, but *B. purpurea* (Jacq.) Ker Gawl. has blackish to dark blue pollen and the anthers have a wider connective that separates the anther lobes (thecae) on the abaxial (fertile) side by a narrow band of dark, sterile tissue. Flowers are scented, often strongly so, with the scent ranging from that of violets, roses, or freesias, to a spicy, acrid to somewhat metallic odor, or combinations of these.

The perianth is typically pale to deep blue or violet, or less often deep pink to purple (*Babiana purpurea*) or pale yellow (*B. odorata* L. Bolus, *B. noctiflora*). The lower lateral tepals have large, white median markings, often edged with dark blue, red, or purple (Table 2), and are held closely together, forming a landing platform. The perianth tube is funnel-shaped, curved to more or less straight, and typically ranges from 6–45 mm long, exceptionally to 60 mm in *B. sambucina* subsp. *sambucina* (Jacq.) Ker Gawl. The tube is divided into a narrow, cylindric lower part usually 6–12 mm long and an expanded funnel-shaped upper part that forms a widening throat ca. 5–8 mm long, which snugly accommodates the upper body of a large bee. The tube contains nectar, which may extend upward a short distance from the base. Occasionally, the lower part of the tube is elongated, but then the lower portion has thick walls and is narrow internally, with the interior blocked by the style so that nectar accumulates well above the tube base, the result of capillary movement. The small amount of nectar is thus forced into the upper half of the tube. The perianth tube may be shorter or longer than the tepals, markedly so in some forms of *B. bainesii* and *B. sambucina* subsp. *sambucina*. In these species, the thick walls of the tube tightly enclose the style and nectar is forced into the upper 10 mm of the slender part of the tube. Such tubes are characteristic of acaulescent species and may be envisaged as functioning as a pseudostem, thus raising the flower above the basal cluster of leaves where it may be more easily seen and visited by insects. This aspect of the perianth tube must be carefully examined before the pollination ecology of such species can be correctly understood.

Flowers of most species in this group are actively visited by apid bees (Table 3), either the native honeybee, *Apis mellifera*, or *Anthophora* species, most commonly *A. diversipes* and *A. rufidicaudis*. *Babiana inclinata* Goldblatt & J. C. Manning is also visited and evidently pollinated by the horsefly *Philoliche atricornis*, which has a proboscis 4–5 mm long, thus comparable with the probosces of apid bees.

Without exception, bees appear to be foraging for nectar and were rarely seen actively scraping pollen from the anthers. Visits are brief, less than two seconds per flower. As a bee forces its body into a flower and inserts its mouthparts down the narrow part of the perianth tube, the dorsal part of its head and thorax come into contact with the anthers or style branches. The dorsal part of the insect becomes covered with pollen, which is transported to other flowers. Despite this passive mode of pollen transfer, bees are often found to carry substantial loads of pollen in their scopae or corbiculae, which must be the result of grooming activity after pollen loads are swabbed on a bee's head and thorax. Bees that visit these *Babiana* flowers are polyphagic foragers (Table 3), and individuals were usually found to carry the pollen of various co-blooming species, most often *Bulbine* Wolf (Asphodelaceae), *Lachenalia* J. Jacq. (Hyacinthaceae), *Lobostemon* Lehm. (Boraginaceae), and other genera of the Iridaceae, both on various parts of their bodies and in their scopae or corbiculae. Curiously, despite this nectar-foraging pattern, all *Apis* individuals collected on *B. ambigua* at two study sites had corbiculae comprising pure loads of *Babiana* pollen.

Nectar characteristics of species belonging to this pollination group have relatively high sugar concentrations, ranging from a mean of 22% sucrose equivalents in *Babiana ambigua* and *B. crispa* G. J. Lewis to a maximum of more than 50% in *B. tritonoides* G. J. Lewis. Standing crop nectar volumes are relatively small, with a range measured in 22 species of 0.3–4.6 μ l (Table 4) per flower and exceptionally 11.0 μ l in one specimen of *B. sambucina* subsp. *sambucina*.

Visits to two members of the *Babiana ambigua* group, *B. cedarbergensis* G. J. Lewis and *B. spiralis* Baker, by the long-proboscid fly *Prosoeca peringueyi* (Table 3) merit mention. Flies actively visited these two species at our study sites but did not contact anthers or stigmatic tips of the style branches with their bodies. This is because the length of the perianth tube is shorter than their proboscis length (16–18 mm in *B. cedarbergensis* and 8–10 mm in *B. spiralis*), while captured flies at both sites had probosces exceeding 38 mm. This fly must be regarded as a nectar thief for these *Babiana* species. None of the flies captured at the *B. cedarbergensis* and *B. spiralis* study sites carried pollen of either species.

The Babiana villosula group. In a second group of bee-pollinated *Babiana* species, the flowers are actinomorphic and rotate, with spreading to widely cupped tepals, and the perianth is uniformly colored blue to mauve or pink (in *B. blanda* (L. Bolus) G. J.

Table 3. Pollen load analysis of captured insects on *Babiana* species. Coleoptera: Scarabaeidae: *Anisochelus* Serville, *Anisonyx* Serville, *Dichelus* Serville, *Lepisia* Serville, *Lepithrix* Serville, *Pachycnema* Serville, *Peritrichia* Burmeister. Hymenoptera: Apidae: *Amegilla* Friese, *Anthophora* Latreille, *Apis* L., *Pachymelus* Smith, *Xylocopa* Latreille; Halictidae: *Lasioglossum* Curtis. Diptera: Nemes-trinidae: *Prosoeca* Schiner, *Moegistorhynchus* Wiedemann. Tabanidae: *Philoliche* Wiedemann. Lepidoptera: Noctuidae: *Syngrapha* Hubner. No sunbirds (*Nectarinia* Illiger) were captured and hence pollen loads were not analyzed.

Plant and insect taxon	No. of insects carrying pollen load(s)	
	Host flower only	Host flower + other sp.
B. ambigua group		
<i>B. ambigua</i>		
<i>Apis mellifera</i> L.	2	0
<i>B. attenuata</i>		
<i>Anthophora diversipes</i> Friese ♀	0	1
<i>Anthophora krugeri</i> Eardley & Brooks ♀	0	1
<i>Amegilla</i> sp. indet. ♀	0	1
<i>Anthophora</i> sp. indet. ♂	1	0
<i>Pachymelus peringueyi</i> Friese ♂	1	0
<i>B. cedarbergensis</i>		
<i>Prosoeca peringueyi</i> Lichtwardt*	0	0
<i>B. fragrans</i>		
<i>Anisonyx ursus</i> Fabricius*	0	4
<i>Anthophora diversipes</i> (not captured)		
<i>B. inclinata</i> site 1		
<i>Philoliche atricornis</i> Wiedemann site 2	5	0
<i>Anthophora diversipes</i> ♀*	0	1
<i>Anthophora krugeri</i> ♀	0	1
<i>B. montana</i>		
<i>Apis mellifera</i>	2	0
<i>B. mucronata</i> site 1		
<i>Anthophora diversipes</i> 2♀ 2♂ site 2	0	4
<i>Apis mellifera</i> *	2	3
<i>B. nana</i>		
<i>Anthophora diversipes</i> ♀	0	2
<i>B. odorata</i> site 1		
<i>Anthophora krugeri</i> ♀	2	3
<i>Apis mellifera</i>	1	0
<i>Anisonyx ditus</i> Peringuey	0	0
<i>B. patula</i>		
<i>Apis mellifera</i>	1	2
<i>Anthophora diversipes</i> ♀	0	1
<i>B. purpurea</i>		
<i>Anthophora rufidicaudis</i> Cameron* ♀	0	2
<i>B. sambucina</i> subsp. <i>sambucina</i> site 1		
<i>Anthophora diversipes</i> ♀ site 2	0	1

Table 3. Continued.

Plant and insect taxon	No. of insects carrying pollen load(s)	
	Host flower only	Host flower + other sp.
<i>Anthophora rufidicaudis</i> * ♀ site 3	0	2
<i>Anthophora flaviscopa</i> Eardley* ♀ site 4	0	2
<i>B. scabrifolia</i> site 1		
<i>Apis mellifera</i> * site 2	0	4
<i>Apis mellifera</i>	0	3
<i>B. scariosa</i>		
<i>Anthophora abrochia</i> Eardley Brooks* ♀	0	3
<i>B. sinuata</i>		
<i>Apis mellifera</i>	1	1
<i>B. spiralis</i>		
<i>Pachymelus peringueyi</i> ♀*	0	2
<i>Prosoeca peringueyi</i> *	0	0
<i>Anthophora diversipes</i> * ♀	0	1
<i>B. tritonioides</i>		
<i>Anthophora flaviscopa</i> ♀*	0	1
<i>B. unguiculata</i>		
<i>Anthophora diversipes</i> ♀*	0	2
Total	18	48
B. villosula group		
<i>B. villosula</i> site 1		
<i>Apis mellifera</i> site 2	2	1
<i>Apis mellifera</i> * site 3	3	0
<i>Apis mellifera</i> *	4	0
Total	9	1
B. framesii group		
<i>B. curviscapa</i> site 1		
<i>Prosoeca peringueyi</i> * site 2	0	3
<i>Prosoeca peringueyi</i> site 4	0	2
<i>Prosoeca peringueyi</i> * site 5	2	2
<i>Prosoeca peringueyi</i> *	0	2
<i>B. ecklonii</i>		
<i>Prosoeca peringueyi</i> *	0	2
<i>B. engysiphon</i>		
<i>Prosoeca peringueyi</i> *	4	0
<i>B. framesii</i> site 1		
<i>Prosoeca</i> sp. indet. 1 site 2	2	3 (1 fly only with pollen of another species)
<i>Prosoeca</i> sp. indet. 1*	0	3
<i>B. geniculata</i>		
<i>Prosoeca peringueyi</i>	0	3
<i>B. latifolia</i>		
<i>Prosoeca peringueyi</i>	2	0
<i>B. praemorsa</i>		
<i>Prosoeca</i> sp. indet. 1	0	3
<i>B. pubescens</i>		
<i>Prosoeca peringueyi</i> *	0	7
<i>B. rigidifolia</i>		

Table 3. Continued.

Plant and insect taxon	No. of insects carrying pollen load(s)	
	Host flower only	Host flower + other sp.
<i>Prosoeca peringueyi</i>	0	2
<i>B. sambucina</i> subsp. <i>longibracteata</i> *		
<i>Prosoeca</i> sp. indet. 1	0	3
<i>B. spathacea</i>		
Noctuid and other moths (none captured)		
<i>B. tubiflora</i>		
<i>Moegistorhynchus longirostris</i> Wiedemann	0	4
<i>B. vanzijliae</i> site 1		
<i>Prosoeca</i> sp. indet. 2	2	0
<i>Apis mellifera</i> *	2	1
<i>Anthophora schulzei</i> Friese 1♀ 1♂ site 2	0	2
<i>Prosoeca</i> sp. indet. 1*	6	0
Total	20	42
<i>B. pygmaea</i> group		
<i>B. angustifolia</i> site 1		
<i>Philoliche atricornis</i> site 2	0	2
Unidentified hopliine	2	5
<i>B. melanops</i> site 1		
<i>Apis mellifera</i>	5	1
<i>Xylocopa rufitarsis</i> Lepeletier 2♂	2	0
<i>Anthophora diversipes</i> ♀	0	2
<i>Anisonyx ursus</i>	4	1
<i>Anisonyx ditus</i> site 2	2	0
<i>Anisonyx ursus</i> * site 3	8	2
<i>Dichelus</i> sp. indet.	12	5
<i>Anisonyx ursus</i>	3	0
<i>B. papyracea</i>		
<i>Anisochelus inornatus</i> Burmeister*	4	1
<i>B. pygmaea</i>		
<i>Lepisia rupicola</i> Serville	5	4
<i>Lepisia</i> cf. <i>lebisi</i> Schein	0	3
<i>B. regia</i>		
<i>Anisonyx ursus</i>	0	8
<i>Lasioglossum</i> (<i>Ctenomia</i>) sp. indet.	0	1
<i>B. rubrocyanea</i>		
<i>Anisonyx ursus</i>	1	0
<i>Lepisia rupicola</i> (Fabricius)	0	2
<i>Pachynema crassipes</i> (Fabricius)	0	1 (3 individuals with no pollen)
<i>Apis mellifera</i>	0	1
<i>Lasioglossum</i> (<i>Ctenomia</i>) sp. indet.	0	1
<i>B. stricta</i> site 1		
<i>Apis mellifera</i>	0	2
<i>Anisonyx ursus</i>	2	1

Table 3. Continued.

Plant and insect taxon	No. of insects carrying pollen load(s)	
	Host flower only	Host flower + other sp.
<i>Lepithrix ornatella</i> Peringuey	6	3
<i>B. villosa</i> site 1		
<i>Lepithrix ornatella</i>	6	5
<i>Peritrichia rufotibialis</i> Schein site 2	0	4
<i>Lepithrix fulvipes</i> Thunberg	5	5
<i>Anisonyx ditus</i>	1	4
Total	68	64
<i>B. patersoniae</i> group		
<i>B. noctiflora</i>		
<i>Syngrapha circumflexa</i> Linnaeus	0	0
<i>B. ringens</i> group		
<i>B. ringens</i> site 1		
<i>Nectarinia violacea</i> Linnaeus	not captured (see Goldblatt et al., 1999)	
<i>B. thunbergii</i>		
<i>Nectarinia fusca</i> Vieillot	not captured (see Goldblatt et al., 1999)	
Grand total	98	155

* Represents a fraction of the total number observed but not collected.

Lewis, not included in our study) either with darker pigmentation toward the tepal bases or paler in the throat. Flowers are lightly scented (*B. leipoldtii* G. J. Lewis, *B. radiata* Goldblatt & J. C. Manning, *B. villosula* (J. F. Gmel.) Ker Gawl. ex Steud). The stamens are symmetrically arranged, with the anthers held erect and surrounding the central style. The flowers close at night and expand again the next morning. Only a small amount of nectar is held near the apex of the floral tube, which is narrowed toward the base with the walls tightly enclosing the style. Of the five species with this floral presentation, we have pollinator observations only for *B. villosula*. The species flowers in the late winter or early spring, often when there are few other plants in bloom. Flowers of all three populations studied were visited by honeybees, *Apis mellifera*, which usually foraged briefly for nectar and then scraped the anthers with their legs, and accumulated uniform loads of the whitish pollen in their corbiculae.

Table 4. Nectar properties of *Babiana* species that produce measurable amounts of nectar. SD = standard deviation; (n) = number of individuals sampled; Fru = fructose; Glu = glucose; Suc = sucrose; n/a = not assessed. Nectar sugar chemistry was analyzed by B.-E. van Wyk. Data for some species are from Manning and Goldblatt (1996) and Goldblatt and Manning (2000).

Species	Volume, µl (n)	Mean, % sugar (SD)	Fructose	Glucose	Sucrose	Mean sucrose/ Glu + Fru (n)
<i>B. ambigua</i> group						
<i>B. ambigua</i>	1.2–1.8 (7)	22.0 (4.0)	n/a	n/a	n/a	n/a
<i>B. attenuata</i>	1.7–2.4 (10)	28.1 (2.2)	n/a	n/a	n/a	n/a
<i>B. cedarbergensis</i>	0.8–1.6 (8)	28.4 (3.0)	n/a	n/a	n/a	n/a
<i>B. crispa</i>	2.8 (1)	22.0	n/a	n/a	n/a	n/a
<i>B. cuneata</i>	1.6–3.4 (10)	28.7 (3.9)	n/a	n/a	n/a	n/a
<i>B. fimbriata</i>	1.7–2.8 (10)	40.1 (4.2)	n/a	n/a	n/a	n/a
<i>B. flabellifolia</i>	0.9–1.8 (2)	25.5 (0.7)	n/a	n/a	n/a	n/a
<i>B. fragrans</i>	1.3–2.7 (10)	35.2 (3.4)	n/a	n/a	n/a	n/a
<i>B. inclinata</i>	0.8–2.8 (10)	36.6 (4.1)	n/a	n/a	n/a	n/a
<i>B. lineolata</i>	0.3–1.6 (7)	39.0 (8.4)	n/a	n/a	n/a	n/a
<i>B. mucronata</i> site 1	1.8–2.2 (3)	30.3 (2.9)	9	16	75	3.0 (1)
site 2	1.4–1.7 (4)	33.5 (3.0)	n/a	n/a	n/a	n/a
<i>B. nana</i>	1.7–2.2 (3)	36.3 (3.8)	n/a	n/a	n/a	n/a
<i>B. odorata</i> site 1	1.0–2.7 (5)	27.4 (5.7)	11	17	72	2.57 (1)
site 2	1.3–2.4 (4)	29.6 (3.1)	n/a	n/a	n/a	n/a
<i>B. patula</i>	1.3–2.1 (10)	42.3 (3.4)	n/a	n/a	n/a	n/a
<i>B. purpurea</i>	0.8–1.9 (10)	32.3 (1.6)	n/a	n/a	n/a	n/a
<i>B. sambucina</i> subsp. <i>sambucina</i> site 1	4.4–11.0 (2)	26.5 (7.8)	3	8	89	8.09 (1)
site 2	3.8–4.6 (10)	28.3 (1.1)	n/a	n/a	n/a	n/a
site 3	1.2–3.2 (10)	28.6 (2.3)	n/a	n/a	n/a	n/a
<i>B. scabrifolia</i> site 1	1.2–2.5 (7)	28.0 (4.3)	n/a	n/a	n/a	n/a
site 2	1.2–1.8 (10)	27.9 (3.1)	n/a	n/a	n/a	n/a
<i>B. scariosa</i> site 1	0.4–1.2 (6)	37.0 (5.6)	n/a	n/a	n/a	n/a
site 2	0.6–1.4 (5)	39.4 (4.5)	n/a	n/a	n/a	n/a
<i>B. sinuata</i>	1.5–2.4 (10)	27.8 (2.6)	n/a	n/a	n/a	n/a
<i>B. spiralis</i>	2.4–3.6 (10)	33.3 (3.7)	n/a	n/a	n/a	n/a
<i>B. tritonioides</i>	0.4–0.6	> 50	n/a	n/a	n/a	n/a
<i>B. unguiculata</i>	0.3–1.9 (5)	31.3 (4.1)	n/a	n/a	n/a	n/a
<i>B. villosula</i> group						
<i>B. leipoldtii</i>	0.6–1.4 (10)	24.2 (1.3)	n/a	n/a	n/a	n/a
<i>B. villosula</i>	< 0.2 (10)	n/a	n/a	n/a	n/a	n/a
<i>B. framesii</i> group						
<i>B. brachystachys</i>	5.3–8.2 (5)	23.4 (1.2)	8–19	24–27	54–58	1.28 (2)
<i>B. curviscapa</i> site 1	4.2–5.9 (3)	28.0 (2.0)	9–12	14–19	58–73	1.78 (4)
site 2	2.0–4.4 (5)	25.0 (n/a)	12	19	69	2.23 (1)
site 3	2.7–6.2 (5)	28.3 (1.2)	n/a	n/a	n/a	n/a
site 4	4.7–2.1 (8)	29.8 (2.3)	n/a	n/a	n/a	n/a
<i>B. dregei</i> site 1	3.9–9.6 (5)	22.0 (2.2)	13–15	19–21	64–68	1.94 (2)
site 2	1.8–4.1 (4)	23.3 (2.2)	n/a	n/a	n/a	n/a
<i>B. ecklonii</i> site 1	4.3–8.9 (5)	27.7 (2.0)	5–11	10–18	72–85	3.29 (3)
site 2	2.7–3.5 (3)	31.7 (1.5)	n/a	n/a	n/a	n/a
<i>B. engysiphon</i>	1.6–4.3 (7)	29.3 (3.1)	n/a	n/a	n/a	n/a
<i>B. framesii</i> site 1	2.6–6.4 (5)	25.5 (0.9)	7–9	12–14	77–81	3.84 (3)
site 2	2.6–3.3 (10)	28.3 (2.2)	n/a	n/a	n/a	n/a
<i>B. geniculata</i>	3.2–4.8 (5)	29.3 (1.2)	17	21	62	1.63 (1)
<i>B. latifolia</i>	1.8–8.8 (10)	29.9 (2.6)	n/a	n/a	n/a	n/a
<i>B. praemorsa</i>	3.9–9.6 (5)	27.0 (1.6)	3–7	10–14	75–79	4.53 (2)
<i>B. pubescens</i>	3.2–4.8 (5)	28.0 (1.7)	3–8	9–14	78–88	2.18 (2)
<i>B. sambucina</i> subsp. <i>longibracteata</i>	3.9–6.6 (3)	30.0 (n/a)	6–12	10–19	69–84	3.48 (3)

Table 4. Continued.

Species	Volume, µl (n)	Mean, % sugar (SD)	Fructose	Glucose	Sucrose	Mean sucrose/ Glu + Fru (n)
<i>B. spathacea</i> site 1	4.3–5.5 (3)	29.3 (1.1)	13–16	16–18	66–71	2.17 (2)
site 2	2.8–4.1 (10)	32.3 (2.6)	16–17	20	63–64	1.74 (2)
<i>B. tubiflora</i> site 1	2.3–5.0 (5)	25.6 (1.1)	9–15	14–22	63–77	2.57 (3)
site 2	4.5–6.2 (10)	24.9 (1.3)	n/a	n/a	n/a	n/a
<i>B. vanzijliae</i> site 1	1.7–2.2 (10)	28.7 (1.8)	12–20	15–17	63–73	2.13 (2)
<i>B. pygmaea</i> group						
<i>B. angustifolia</i>	not detectable					
<i>B. melanops</i> site 1	0.8–1.8 (10)	24.2 (1.3)	n/a	n/a	n/a	n/a
site 2	not detectable					
site 3	not detectable					
<i>B. pygmaea</i>	not detectable					
<i>B. regia</i>	trace					
<i>B. rubrocyanea</i>	trace					
site 2	0.6–1.4 (10)	33.9 (2.9)	n/a	n/a	n/a	n/a
<i>B. stricta</i> site 1	trace					
<i>B. villosa</i>	trace or none					
	evidently produced					
<i>B. patersoniae</i> group						
<i>B. noctiflora</i>	4.8–6.2 (10)	30.6 (3.5)	n/a	n/a	n/a	n/a
<i>B. patersoniae</i>	1.7–2.8 (5)	31.7 (1.6)	2–5	4–9	86–94	8.34 (3)
<i>B. virginea</i>	17–22 (3)	26.0 (1.0)	n/a	n/a	n/a	n/a
<i>B. ringens</i> group						
<i>B. carminea</i>	21.0–26.0 (3)	21.0 (2.6)	n/a	n/a	n/a	n/a
<i>B. ringens</i> site 1	19.5–23.4 (2)	23.0	9	20	71	2.45 (1)
site 2	25.0–28.0 (2)	23.5 (0.7)	12–13	17	70–71	2.39 (2)
<i>B. thunbergii</i>	24.0–30.0 (10)	25.5 (0.8)	15–21	18–25	60–65	1.65 (4)

Nectar of this pollination group has relatively modest sugar concentrations, with a mean of 24.2% sucrose equivalents in *Babiana leipoldtii*, the only species in the group for which we have data (Table 4). Standing crop nectar volumes are relatively small, with 0.6–1.4 µl measured in *B. leipoldtii*, or negligible.

The Babiana framesii group. In a third group, the flowers are zygomorphic in 17 species and actinomorphic in one more. Zygomorphic flowers have either a bilabiate perianth with the dorsal tepal erect and the lower tepals forming a platform, or the tepals spread equally with the dorsal tepal being somewhat larger and held apart from the others (Fig. 2A–E). All three lower tepals or just the lower laterals have pale contrasting markings. As in the *Babiana ambigua* group, the style and stamens are unilateral and lie arched over the lower tepals, with the anthers facing the landing platform. The style divides opposite to or slightly beyond the anther apices, and the style branches arch outward. The stigmatic ends of the style branches are thus held away from the anthers and pollen. Most distinctive of this group, the lower part of the perianth tube is elongated, usually hollow to the base, typically 35–70 mm long, or exceptionally to 80 or 90 mm in *B.*

tubiflora (Burm. f.) Ker Gawl. and *B. tubulosa* (Burm. f.) Ker Gawl. The flowers are usually scentless (Table 2) or rarely strongly scented (*B. sambucina* subsp. *longibracteata* G. J. Lewis, *B. dregei* Baker, *B. vanzijliae* L. Bolus). As in the *B. ambigua* group, the flowers close at night and expand again the next morning. Flowers of the group have three quite different pigmentation patterns that are closely correlated with the insects that pollinate them.

The flowers produce relatively large amounts of sucrose-dominant nectar (Table 4). Volumes measured in 14 species range from 1.6 µl in *Babiana engysiphon* J. C. Manning & Goldblatt to 9.6 µl per flower in populations of *B. dregei* and *B. praemorsa* Goldblatt & J. C. Manning. Nectar sugar concentrations are relatively high, ranging from a mean of 22.0% sucrose equivalents in *B. dregei* to maxima of 30.0% in *B. sambucina* subsp. *longibracteata* and 32.3% in *B. spathacea*.

The perianth is usually predominantly blue to violet (Table 2), intensely so in *Babiana praemorsa*, and exceptionally red-purple in northern Namaqualand populations of *B. curviscapa* G. J. Lewis, and the lower tepals are marked with white, longitudinal diamond- to spear-shaped marks edged proximally in darker blue, purple, or red.

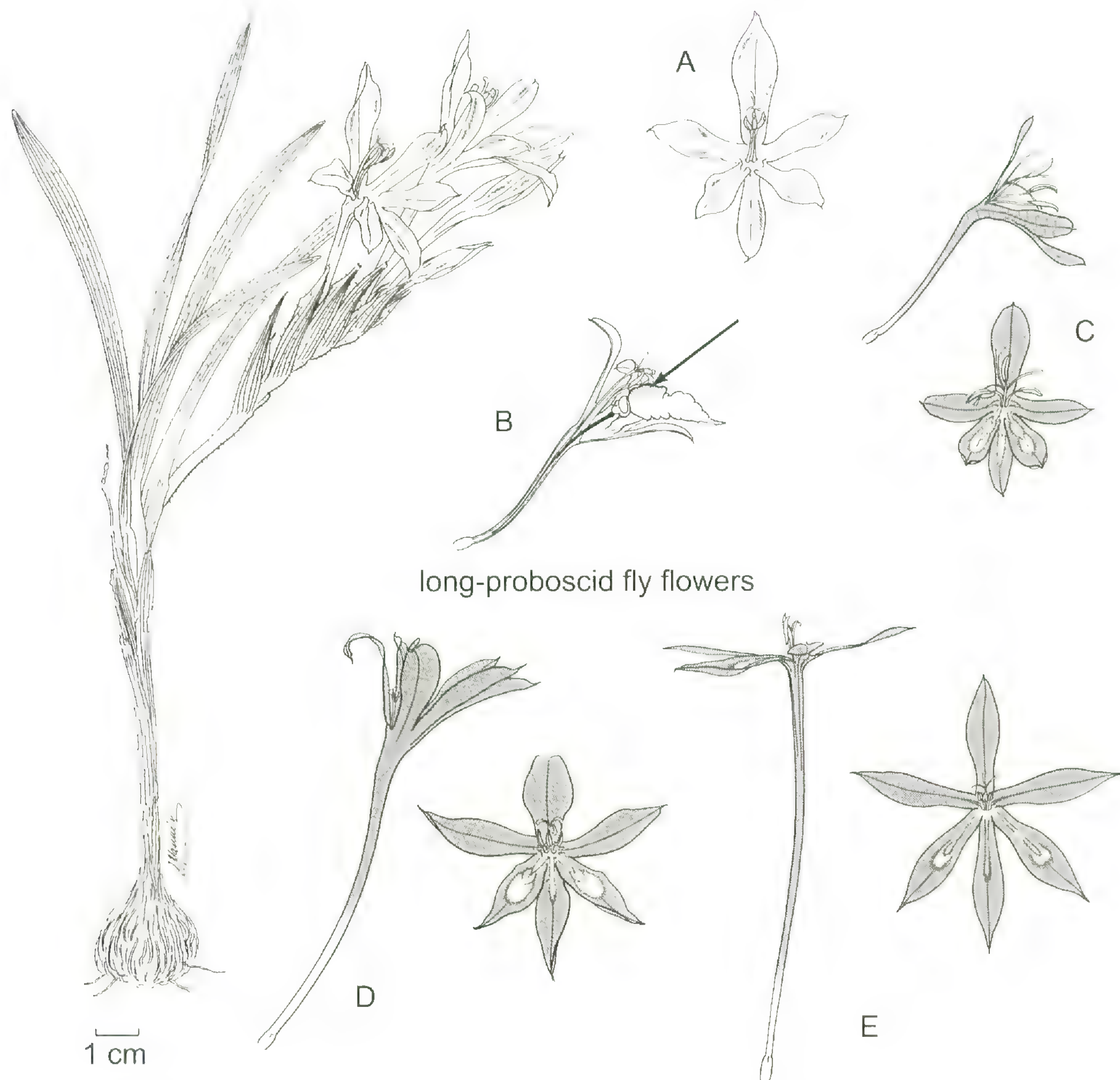


Figure 2. Flowers of *Babiana* species pollinated by long-proboscid flies. —A. Plant of *B. engysiphon*, showing long-tubed flowers, and front view of flower. —B. *Babiana curvicauda*, longitudinal section of flower showing orientation of *Prosoeca* fly when foraging for nectar; arrow indicates part of the fly's body that will contact anthers or style branches. —C–E. Lateral and front view of flowers of (C) *B. geniculata*, (D) *B. framesii*, (E) *B. praemorsa*, with shading for violet coloration, lower lateral tepals bearing pale markings (putative nectar guides). Drawn by John Manning from live plants. Scale bar = 1 cm; D and E, approximately 2× scale bar.

In a second species cluster in the *Babiana framesii* L. Bolus group, which includes the common West Coast *B. tubiflora*, as well as *B. tubulosa* and the rare Namaqualand *B. brachystachys* (Baker) G. J. Lewis, the perianth is white, often flushed pink on the outside, with dark pink to red markings on the lower tepals. We include *B. spathacea* in this group, noting that no long-proboscid fly has ever been collected over its range in the Western Karoo (Goldblatt & Manning, 2007). The only insects captured on the species are moths (Table 3), but we consider these opportunistic visitors, as moth flowers are always scented and often close during the day. It is possible the legitimate fly pollinator of *B. spathacea* is extinct.

Exceptionally, *Babiana vanzijliae* usually has a predominantly yellow perianth, sometimes flushed light

mauve outside or on fading. We include it in the *B. framesii* group with some hesitation, not only because of the predominant yellow perianth color, but because the flowers are scented and the perianth tube is sometimes intermediate in length between those of typical members of the *B. ambigua* and *B. framesii* groups, ranging from 25–35 mm long, the narrow lower part 15–25 mm long.

The length of the perianth tube in some species in this group does not always reflect the length of the mouthparts of legitimate insect visitors. In *Babiana dregei*, the tube may be 50–65 mm long, but the lower portion of the tube has thick, fleshy walls and a narrow interior that is filled by the style (Manning & Goldblatt, 1996). Nectar is thus forced higher up the tube, where it is available to insect visitors with

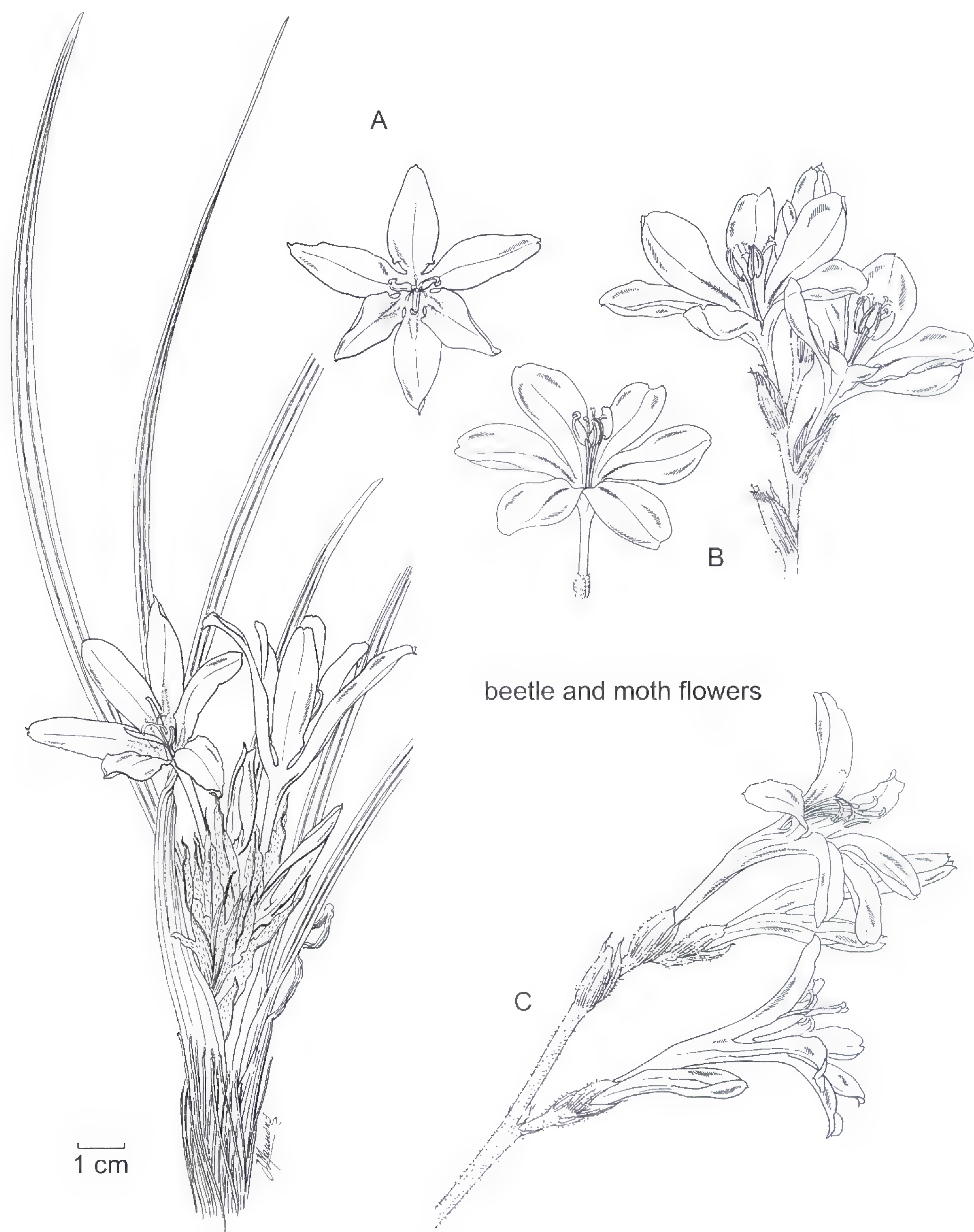


Figure 3. Flowers of *Babiana* species pollinated by (A, B) hopliine beetles and (C) moths. —A. Plant of *B. papyracea* and top view of the radially symmetric flower. —B. *Babiana melanops*, with portion of the inflorescence and a single flower. —C. *Babiana noctiflora*, with inflorescence and side view of flowers showing the elongate perianth tube. Drawn by John Manning from live plants. Scale bar = 1 cm.

mouthparts exceeding 30 mm in length, less than the total length of the tube.

Most species in this group are pollinated exclusively by long-proboscid flies of the family Nemestrinidae. As described in *Lapeirousia* (Goldblatt et al., 1995) and *Sparaxis* (Goldblatt et al., 2000a), flowers in western

southern Africa with long floral tubes and vivid, blue to purple flowers with white nectar guides are likely to be pollinated by one of two species of the genus *Prosoeca*, *P. peringueyi* or *Prosoeca* sp. 1, and this is the case in *Babiana*. Four species of the genus have already been reported as being pollinated by one of these two fly

species (Manning & Goldblatt, 1996; Goldblatt & Manning, 2000), and we add eight more to the list here.

We infer that the few species with white flowers with pink or red markings are adapted for pollination by a third nemestrinid fly, *Moegistorhynchus longirostris*, as are similarly proportioned and pigmented flowers in *Lapeirousia* (Goldblatt et al., 1995; Manning & Goldblatt, 1997) and *Gladiolus* (Goldblatt & Manning, 1999). This fly is restricted to the west coast and near interior of southern Africa, and this corresponds exactly to the range of the white- to pink-flowered, long-tubed species of *Babiana*. Our only observation for this cluster of species is for *B. tubiflora*, published elsewhere as *B. tubulosa* var. *tubiflora* (L. f.) G. J. Lewis (Manning & Goldblatt, 1997).

Both *Prosoeca* and *Moegistorhynchus* are polylectic foragers (Manning & Goldblatt, 1996, 1997; Goldblatt & Manning, 2000; Johnson & Steiner, 1997), and individuals were found to carry the pollen of co-blooming species with similar floral morphology, including *Pelargonium* L'Hér. ex Aiton (Geraniaceae), *Geissorhiza* Ker Gawl., *Gladiolus*, and *Lapeirousia* (all Iridaceae), and *Disa* P. J. Bergius (Orchidaceae) (Table 3). The long-tubed species of *Babiana* thus belong to one of two discrete guilds of plant species that share a similar floral appearance, the *Prosoeca peringueyi* or *Moegistorhynchus* pollination guilds as defined by Manning and Goldblatt (1996, 1997). The elongated probosces of these flies are typically slightly longer than the length of the perianth tubes (or at least the hollow portion of the tube) of the plant species that they visit, but the flies are the only insects that are able to forage on the nectar held in the lower part of the perianth tube.

As we have described in detail elsewhere (Goldblatt & Manning, 1999, 2000), flies grasp the tepals with their tarsi and probe for nectar while continuing to vibrate their wings. As they force their bodies into the flower, pollen is passively deposited on specific parts of their bodies, in the case of *Babiana* species usually in the dorsal part of the thorax (Fig. 2B). In *B. geniculata* G. J. Lewis, in which the anthers are held well apart from one another (Fig. 2C), pollen deposition may be on the dorsal or lateral parts of the thorax (Manning & Goldblatt, 1996). Visual observation and pollen load analysis show that all fly species visit flowers of a range of other species during foraging bouts, most of which have morphologically convergent flowers that may be regarded as belonging to the same pollination guilds (Manning & Goldblatt, 1996).

Thus, *Prosoeca peringueyi* visits dark red, purple, or dark blue flowers of *Pelargonium crassicaule* L'Hér., *P. magenteum* J. J. A. van der Walt, *P. sericifolium* J. J. A. van der Walt, and species of Iridaceae including

Hesperantha latifolia (Klatt) M. P. de Vos, *Lapeirousia jacquinii* N. E. Br., and *L. silenoides* (Jacq.) Ker Gawl., as well as co-blooming *Babiana curviscapa*, *B. dregei*, *B. ecklonii* Klatt, *B. engysiphon*, *B. framesii*, *B. geniculata*, *B. pubescens* (Lam.) G. J. Lewis, and *B. rigidifolia* Goldblatt & J. C. Manning, at sites in Namaqualand and Western Cape. A second fly, *Prosoeca* sp. 1, visits the red, purple, or violet flowers of species of Iridaceae including *H. oligantha* (Diels) Goldblatt, *L. oreogena* Schltr. ex Goldblatt, *L. jacquinii*, and *Romulea hantamensis* (Diels) Goldblatt, as well as co-blooming *B. praemorsa* (published as *B. flabellifolia* Klatt), *B. framesii*, and *B. sambucina* subsp. *longibracteata* (Manning & Goldblatt, 1996), at sites on the Bokkeveld Escarpment and Hantam Mountains. Likewise, along the west coast of Western Cape, *Moegistorhynchus longirostris* visits white, cream, or pink flowers of *P. longicaule* Jacq., *Disa draconis* (L. f.) Sw. (Orchidaceae), and several other Iridaceae including *Geissorhiza exscapa* (Thunb.) Goldblatt, *Gladiolus angustus* L., *L. anceps* (L. f.) Ker Gawl., and *Ixia paniculata* D. Delaroche, as well as *B. tubulosa* (Manning & Goldblatt, 1997; Goldblatt & Manning, 2000).

Exceptional for the *Babiana framesii* group in pigmentation and floral odor, *B. vanzijliae* has predominantly yellow flowers that, to the human nose, have a strong odor that represents a combination of violets and an unpleasant, acrid, insecticide-like component, for convenience here called spicy musk (e.g., Table 2). The flowers do, however, produce ample quantities of nectar, retained in the lower part of the tube and accessible only to two captured visitors, *Prosoeca* sp. 1 and a second undescribed *Prosoeca* species (*Prosoeca* sp. 2) with a proboscis 12–14 mm long (tube length at this study site was 30–35 mm). The flowers were also visited at this site by *Apis mellifera* workers and *Anthophora schulzei* (Table 3). Both bees attempted unsuccessfully to forage for nectar, but in doing so became covered in the yellow pollen of *B. vanzijliae*, thus accomplishing pollen transfer in the process. For these bees, the flowers of *B. vanzijliae* appear to function as mimics of the flowers of other species from which they do obtain nectar. *Prosoeca* sp. 1, which forages more frequently on the long-tubed purple flowers of *B. framesii*, *B. sambucina* subsp. *longibracteata*, *Lapeirousia jacquinii*, and *L. oreogena* that grow nearby, successfully pollinated *B. vanzijliae* with longer-than-usual perianth tubes at a second study site. Here, flowers had perianth tubes 35–50 mm long, while flies had probosces 31–44 mm long (mean 36.9 mm, standard deviation 4.4, $n = 15$). Plants with shorter perianth tubes that were visited by flies with longer-than-average-length probosces, however, were not pollinat-

ed by visiting flies. Their probosces were so long that when inserted to their full extent into the tube, their bodies did not contact either anthers or stigmas. Variation in the perianth tube of *B. vanzijliae* is notable. While plants at study site 1 have a tube 30–35 mm long, plants at our second study site had a tube 35–50 mm long. We suspect that the perianth tube length in flowers of *B. vanzijliae* may be tracking the proboscis length of local pollinators.

Visits to two members of the *Babiana ambigua* group, *B. cedarbergensis* and *B. spiralis*, by the long-proboscid fly *Prosoeca peringueyi* (Table 3) are discussed above under the *B. ambigua* group. We regard them as nectar thieves of these two species.

The Babiana pygmaea group. A fourth pollination group includes *Babiana melanops*, *B. pygmaea* (Burm. f.) Baker, *B. regia* (G. J. Lewis) Goldblatt & J. C. Manning, *B. rubrocyanea* (Jacq.) Ker Gawl., *B. stricta*, *B. villosa*, and a few more (Table 2) that have a salver- or bowl-shaped, radially symmetric perianth, sometimes marked with a contrasting, usually darker center, or possessing purple-black anthers with an expanded connective (Fig. 3A, B). These flowers may have a relatively short tube, 10–20 mm long, or an elongate tube up to 45 mm long, either containing only a trace of nectar near the apex or evidently no nectar. In species with longer tubes, the tube is filled internally by the style, which is closely sheathed by the thick walls of the tube. Nectar, when present, is thus restricted to the upper part of the tube. The tepals, up to 25 mm long, spread horizontally or arch slightly upward to form a shallow bowl. These flowers close in the late afternoon, and the tepals then cover the stamens and style branches. The tepals unfold again during late morning in warm weather. Perianth color is brilliant red to purple in *B. villosa*, bluish to violet with a blue-black center in *B. melanops*, or deep blue with a bright red center in *B. regia* and *B. rubrocyanea*. *Babiana pygmaea* has a large yellow perianth with a brownish to dull purple center. *Babiana stricta* is exceptional here in comprising populations with pinkish purple, blue-violet, or creamy white flowers, and, while the perianth is radially symmetric, the lower tepals have obscure darker markings toward the base. In *B. stricta* and *B. rubrocyanea* (Table 4), the flowers also produce measurable amounts of nectar.

The style is central and erect and surrounded by symmetrically disposed stamens in most of these species, but in *Babiana rubrocyanea* and *B. stricta* the stamens are unilateral and held to one side of the flower. Style branches are sometimes slender (as in most species of the genus), but the tips are enlarged and prominent in *B. rubrocyanea*, *B. villosa*, and often in *B.*

melanops. The style divides below the base of the anthers or opposite the base to the middle of the anthers with the style branches then extending between the filaments or anthers. Species typically have dark-colored anthers and pollen, usually blackish or dark blue or, in *B. regia* and *B. rubrocyanea*, reddish brown. *Babiana melanops*, *B. stricta*, and *B. villosa* have large anthers, the connective of which is expanded so that the anther thecae are widely separated from one another. Flowers are usually unscented, but those of *B. stricta* are lightly sweet scented and in the southernmost population of *B. melanops* flowers have a light, pleasant odor of violets. The flowers of this population are the only ones in the species that also produce nectar in measurable quantities (Table 4).

Species of this group are visited predominantly by hopliine scarab beetles (Scarabaeidae: Rutelinae: Holpiini). *Babiana rubrocyanea* is visited by two beetle species, *Pachycnema crassipes* and *Anisonyx ursus*, and *B. melanops* is visited by a range of hopliine beetles depending on locality (Table 3), including *A. ursus* alone, or together with *A. ditus*, but the nectar-producing population is visited by a range of bees foraging for nectar as well as by occasional hopliines. *Babiana pygmaea* is visited by *Lepisia rupicola* and *Lepisia* cf. *lebisii*, while *B. regia* was visited at our study site by *Anisonyx ursus*.

The flowers of the *Babiana pygmaea* group have the stereotypical adaptations for the hopliine beetle pollination system described by Steiner (1998) and Goldblatt et al. (1998b): a large, bowl- or salver-shaped flower, constricted perianth tube containing little or no nectar, and bold, contrasting colors. The so-called beetle marks may be represented by different bands or blotches of color on the tepals or by enlarged dark anthers (*B. melanops*, *B. villosa*). *Anisonyx*, *Lepisia*, and *Pachycnema* species, and other hopliines spend between 12 seconds and 10 minutes (or longer) in a flower, either crawling about or at rest with their head directed toward the center of the perianth. Some visits last throughout the night as beetles take refuge in the closed flower until the next day.

Beetles captured on the flowers of these plants are invariably covered with the reddish brown or black pollen of the *Babiana* species and sometimes also pollen of some co-blooming taxa. Hopliine beetles use the flowers as sites for assembly, intraspecific competition, and mating, and although they feed on pollen and sometimes other floral tissue, they do little or no damage to flowers (Steiner, 1998; Goldblatt et al., 1998b).

The open perianth of species of the *Babiana pygmaea* group may also be visited by bees, and we have noted occasional visits to *B. regia* and *B. rubrocyanea* by unnamed species of *Lasioglossum*

(*Ctenomia*) (Halictidae) (Table 3). *Babiana stricta* appears to use both bees and hopliine scarab beetles equally, and while the spreading tepals that are held more or less horizontally seem well-suited to the preferences of beetles, the fragrance and presence of nectar provide an attractant and reward more typical of bee-pollinated flowers.

The Babiana patersoniae group. A small group of species, including *Babiana noctiflora*, *B. patersoniae*, and *B. virginea*, have intensely scented, white or cream to pale yellow or pale blue flowers, sometimes with light purple or pinkish markings on the lower tepals, and a long, cylindric, or weakly tapering perianth tube, 33–50 mm long in *B. noctiflora* (Fig. 3C) and 60–65 mm in *B. virginea* (Table 2). The flowers are unusual in the genus in remaining open at night, and all produce a complex, sweet-spicy odor. Flowers produce ample amounts of nectar, up to 6.2 μ l in *B. noctiflora*, with relatively high sugar concentration (mean 26.0–31.7 sucrose equivalents) (Table 4). In the one species of the group examined for pollinators, *B. noctiflora*, the flowers are visited by long-proboscid moths. The single species of moth captured, *Syngrapha circumflexa* (Noctuidae), has a proboscis 16–17 mm long. Moths are active after dark and crawl over the flowers on an inflorescence, accumulating pollen deposited from the open flowers of each branch on which they alight.

The Babiana ringens group. Two species of the Namaqualand coast and Western Cape Province, *Babiana ringens* and *B. thunbergii*, have morphologically complex flowers with a bright scarlet-red perianth, strongly unequal tepals, and an elongate, sharply curved perianth tube, narrow in the lower half, abruptly expanded in the middle, and wide and cylindric above. The flowers are borne on horizontal branches and face away from the main stem, either well above ground in *B. thunbergii* or at ground level in *B. ringens*. In *B. ringens*, the main stem is represented by a stout, sterile stalk. The dorsal tepal is large and erect, with the margins curved inward partly enclosing the stamens and style, while the upper lateral and lower tepals spread outward. The style and stamens are unilateral and curved upward to lie close to the dorsal tepal, which partly encloses the unusually rigid filaments and style, both of which are dark red. The anthers are well-exserted and dark blue-black, and the elongate style divides well above the exerted anthers. The flowers are unscented and secrete large quantities of nectar, up to 30 μ l in our study population of *B. thunbergii*. Mean nectar concentrations range from 23.0%–25.5% sucrose equivalents in these two species (Table 4).

Flowers of these two species are visited exclusively by sunbirds, *Nectarinia* species. Birds perch on the branches in *Babiana thunbergii* and either on the sterile main axis in *B. ringens* or sometimes on the ground; they push their bills into the upper part of the perianth tube and, evidently, take nectar from the narrow part of the tube with their tongues. We did not capture any sunbirds and so cannot say whether they carried pollen or not. Their foraging, however, invariably results in their head or neck contacting the anthers and style branches. This is clearly evident in published photographs of *N. famosa* visiting both *B. thunbergii* and *B. ringens* in the wild (Cowling & Pierce, 1999: 129; Manning, 2004: 115). Because sunbirds are the only animal visitor to these flowers, they must be assumed to be their sole pollinators.

We include the southern Namaqualand species, *Babiana carminea* J. C. Manning & Goldblatt in the *B. ringens* group, although it is clearly taxonomically distantly related to the other two members of the group and has an acaulescent growth habit. Like these two species, the flowers are red and have an elongate tube with the upper part relatively wide. We have no pollinator observations, but the flowers produce large amounts of nectar of relatively low sugar concentration, a feature that is also consistent with sunbird pollination.

NECTAR

Nectar glands are septal, as they are in the entire subfamily Crocoideae (Goldblatt, 1990; Rudall et al., 2003). Nectar is secreted from three minute pores at the top of the ovary (one per chamber) directly into the base of the perianth tube, where accumulated fluid is retained until removed by a foraging insect. In several species, the lower part of the tube may be extremely narrow internally, the walls thus tightly enveloping the style (see discussion above) so that nectar is forced by capillary action higher up the tube, sometimes to within a short distance of the tube mouth. Notable examples are acaulescent species including the long-tubed *Babiana attenuata* G. J. Lewis, *B. dregei*, forms of *B. bainesii*, and *B. sambucina*. Effective tube length for foraging insects is much less than the total tube length because, at least in *B. attenuata*, *B. bainesii*, and *B. sambucina*, nectar lies within 10 mm of the base of the wider part of the tube, where it is accessible to most anthophorine bee species. Such long tubes function partly to raise the flower above the rosette of basal leaves, as well as being reservoirs of nectar.

Measurable volumes of nectar are produced in most species, and volume correlates with the length of the

hollow part of the tube (Tables 2, 4). The long-tubed *Babiana ringens* and *B. thunbergii* produced the most nectar, 25.0–28.0 μl in the former in flowers undisturbed by pollinators (the perianth had not fully expanded when nectar was measured) and 24.0–30.0 μl of nectar in the latter, while flowers of the *B. pygmaea* group, pollinated largely or exclusively by hopliine beetles, have the smallest amounts of measurable fluid or evidently none at all. *Babiana melanops* and *B. rubrocynaea*, with up to 1.8 μl or 1.4 μl of nectar, respectively, are exceptional here, but they have a mixed system, using both hopliines and bees. Species pollinated by large-bodied bees offer nectar mainly in the 0.4–3.6- μl range, but as much as 11.0 μl of nectar was produced by a sample of *B. sambucina*. Most species pollinated by long-proboscid flies and moths offer 1.6–9.6 μl of nectar, considerably less than the 19–30.0 μl of nectar offered by sunbird-pollinated species. Putatively moth-pollinated *B. virginea*, however, is exceptional in offering nectar in the 17.0–22.0- μl range.

Nectar sugar analyses of *Babiana* species indicate that all species offer nectars that are sucrose dominant (sensu Baker & Baker, 1983), with the ratio of sucrose to hexose sugars greater than 1 (Table 4). There is, however, a fair degree of variation in the sucrose to hexose ratio, with the bird-pollinated *B. ringens* and *B. thunbergii* producing nectar with sucrose to hexose ratios between 1.65 and 2.45 (Table 4), whereas some long-proboscid fly-pollinated and bee-pollinated species have ratios above this range, sometimes with the ratio greater than 8 in one sample of *B. sambucina* subsp. *sambucina*, as well as in the putatively moth-pollinated *B. patersoniae*.

As noted in other genera of Iridaceae, including *Gladiolus*, *Hesperantha* Ker Gawl., *Ixia* L., and *Sparaxis*, nectar sugar concentration correlates only to a limited extent with pollinator type (Goldblatt et al., 1998a, 2000a, b, 2001, 2004b; Goldblatt & Manning, 1999, 2000). Thus, species pollinated by nectar-foraging anthophorine bees and *Apis mellifera* have nectar concentrations ranging from 22.0%–42.3% sucrose equivalents with an exceptional more than 50% in *B. tritonioides*. Among these species, *B. fimbriata* (Klatt) Baker and *B. patula* N. E. Br. also stand out in having unusually concentrated nectar for a bee-pollinated species, 40.1%–42.3% sucrose equivalents.

In long-proboscid fly-pollinated species of *Babiana*, nectar concentration is typically in the 24.0%–30.0% range, with a high reading in *B. spathacea* of 32.3% sucrose equivalents. Bird-pollinated species have slightly more dilute nectar, 21.0–25.5 sucrose equivalents, a characteristic noted for this pollination system in other genera of the Iridaceae, including

some species of bird-pollinated *Gladiolus* (Goldblatt et al., 1999, 2001).

Moth-pollinated (or presumed moth-pollinated) species produce nectar of 26.0%–31.7% mean sucrose equivalents, lower than that encountered in moth-pollinated species of *Gladiolus* and *Hesperantha*, which, in the latter, may exceed 50% (Goldblatt & Manning, 2002; Goldblatt et al., 2004b).

COMPATIBILITY RELATIONS

Only one species studied, *Babiana tubulosa*, showed full self-compatibility and autogamy. Plants set full complements of mature capsules, evidently containing viable seeds when isolated from visiting insects and without hand pollination. Capsules appeared normal, as did seeds, but we did not conduct viability tests. The remaining seven species for which compatibility relations were examined proved self-incompatible. These included *B. ambigua*, *B. attenuata*, *B. curviscapa*, *B. fourcadei* G. J. Lewis, *B. latifolia* L. Bolus, *B. odorata*, and *B. patula*. No capsules were produced in hand-pollinated flowers. Compatibility relations are known in one more species, the sunbird-pollinated *B. ringens* (Anderson et al., 2005), which is a facultative self-pollinator.

From this limited sampling, we cautiously suggest that self-incompatibility may be the rule in the genus and that facultative autogamy occurs in at least two species with specialized pollination systems, although not in the above two long-proboscid fly-pollinated species, *Babiana curviscapa* and *B. latifolia*.

DISCUSSION

POLLINATOR DIVERSITY

Early observations on the pollination biology of *Babiana* were limited to less than a handful of species. These included visits to *Babiana plicata* Ker Gawl. (probably what is now *B. fragrans* (Jacq.) Ker Gawl.) by the hopliine beetle *Anisonyx ursus*, reported by Scott Elliot (1891), who also noted visits by *A. ursus* to a species he called *B. spathacea* in a population near Cape Town. From the illustration provided, this is probably *B. ambigua*. In addition, Marloth (1898, 1915) first recorded visits to flowers of *B. ringens* by the sunbird, *Nectarinia violacea*, and followed Scott Elliot (1890) in concluding that the species was pollinated by these birds. Until then, this assumption had been based solely on inferences drawn from floral morphology.

These preliminary observations did not even begin to show the diversity of pollination systems in the genus. Vogel (1954), in his mammoth review of pollination systems in southern Africa, concluded that

species of *Babiana* were pollinated predominantly by bees (though he made no personal observations of insect visitors to the genus). He also inferred that *B. tubiflora* was pollinated by the same long-proboscid fly as *Lapeirousia fabricii* (D. Delaroche) Ker Gawl. (i.e., *Moegistorhynchus longirostris*), and that *B. bainesii* probably had this same pollination system, which he called psychophily (pollination by day-flying butterflies), a category in which he included long-proboscid fly pollination. Vogel also recognized that *B. ringens* was pollinated by sunbirds. More recently, *B. thunbergii* (as *Antholyza plicata* L. f.) as well as *B. ringens* were regarded by Rebelo (1987) as pollinated by sunbirds in his review of that pollination system in the Cape flora (i.e., the greater part of the winter-rainfall climate zone flora of southern Africa).

Pollination in *Babiana* is, in fact, considerably more diverse than hitherto suggested. As we have shown for other African genera of the Iridaceae, pollination systems in *Babiana* are closely correlated with floral structure, pigmentation patterns, timing of anthesis, scent characteristics, and nectar secretion (Goldblatt et al., 1995, 2000a, b, 2001, 2004b). In general, the radiation of pollination systems in *Babiana* closely parallels that found in other larger genera of the Iridaceae in southern Africa, in particular, of subfamily Crocoideae (syn. Ixioideae). Pollination by *Apis* and large-bodied and long-tongued anthophorine bees is the most common system in *Babiana* and most likely the ancestral one. The system exactly parallels that recorded in *Gladiolus* (ca. 167 species in southern Africa), which have a pollination system in which a species is dependent on one or two species of anthophorine bee, or sometimes *Anthophora* and worker honeybees, for its pollination (Goldblatt et al., 1998a). The same system has also been reported for the southern African genera *Hesperantha* (ca. 80 species), *Ixia* (ca. 52 species), and *Sparaxis* (15 species) (Goldblatt et al., 2000a, b, 2004b). In *Babiana*, 18 species have been shown to be pollinated by large-bodied and long-tongued anthophorine bees and *Apis mellifera*. Another 35 species have flowers of this type, thus 53 species (58% of the genus) are inferred to share this pollination system. One of these species, *B. fragrans*, seems as often visited and effectively pollinated by hopline scarab beetles. The presence of a strong floral scent and ample nectar in *B. fragrans* flowers seems to suggest that bee pollination is the more important system in the species. Hopline visitors may simply be opportunistic, for the relatively small area offered by the outspread tepals seems poorly suited to the activity of the relatively large *Anisonyx ursus* captured on them.

As in *Gladiolus*, bee pollination comprises two contrasting systems (Goldblatt et al., 1998a; Bernhardt & Goldblatt, 2000) with floral characters and floral dimensions correlating with bee size, proboscis length, and foraging behavior. The dominant one is a passive pollination system, discussed above, where bees foraging for nectar in gullet flowers (in the terminology of Faegri & van der Pijl, 1979) passively accumulate loads of pollen on the dorsal part of the head and thorax, subsequently to be transferred to receptive stigmas of other flowers. A second bee pollination system involves flowers with an actinomorphic perianth, radial symmetry, and prominently displayed anthers where bees actively collect pollen, although nectar is also offered. Again, as in *Gladiolus*, the flowers of *Babiana* species with this second bee pollination system are inferred to be secondarily radially symmetric, and the active pollination system is derived and less frequent than the passive one. Another similarity with *Gladiolus* is that bee-pollinated flowers in *Babiana* are usually strongly fragrant. One species, *B. villosula*, has been confirmed to be pollinated by *Apis mellifera* foraging for pollen, and four more species (Table 2) share this type of flower (6% of the genus). One population of *B. melanops* also has this pollination system, in which *Anthophora diversipes* and the anthophorine, *Xylocopa rufitarsis*, actively visit flowers for nectar and pollen. Elsewhere, this species is pollinated exclusively by hopline beetles (Table 3), and the flowers lack fragrance and nectar. Two species, *B. rubrocyanea* and *B. stricta*, are visited by a combination of hoplines and bees (Table 3), and both offer small quantities of nectar as well as pollen. We regard these two species and *B. fragrans* (see above) as having a mixed or bimodal pollination system (Table 5).

Like other large genera of subfamily Crocoideae, pollination by long-proboscid flies is important in *Babiana*. Thirteen taxa (12 species and one subspecies) have been recorded to be visited by long-proboscid nemestrinids, species of *Prosoeca* or *Moegistorhynchus longirostris*, all of which can be seen to brush against anthers and stigmas and carry visible loads of pollen (Table 3). This pollination system is inferred for an additional five species with virtually identical floral presentation. Thus, a total of 18 taxa (20% of the genus) are pollinated by long-proboscid flies, most of them exclusively. Of these, only *B. vanzijliae* may have a mixed system, with some populations with a shorter perianth tube being effectively pollinated by bees as well as long-proboscid flies, although the bees were not able to access nectar. Pollination by long-proboscid flies is the second most important pollination strategy in both southern African *Gladiolus* and *Babiana*, with 18% of

Table 5. Frequency and taxonomic distribution of pollination systems in *Babiana*. The genus comprises 90 species distributed in three sections, all assumed to be monophyletic (Goldblatt & Manning, 2007); n/a = not applicable. For scoring purposes, *B. sambucina* subsp. *sambucina* and subsp. *longibracteata* are scored separately with the result that a total of 91 species are included in the table.

Pollination system	Total species confirmed	Total confirmed and inferred	Taxonomic sections	Taxonomic series
Large-bodied, long-tongued bees (Apidae s.l.)	18	53 (58%)	3	8
Short-tongued (or pollen-collecting) bees	1	5 (6%)	2	2
Long-proboscid fly	13	18 (20%)	2	4
Passerine bird	2	3 (3%)	2	2
Moth	1	3 (3%)	2	4
Hopliine beetle	6	6 (7%)	2	3
Hopliine beetle/pollen-collecting female bee	3	3 (3%)	1	1
Total	44	91 (100%)	n/a	n/a

Gladiolus species in the subcontinent having this pollination system (Goldblatt et al., 2001). Long-proboscid fly pollination also occurs in several other genera of Iridaceae subfamily Crocoideae, including *Geissorhiza*, *Hesperantha*, *Lapeirousia*, *Radinosiphon* N. E. Br., *Romulea* Maratt., *Tritonia* Ker Gawl., *Tritoniopsis* L. Bolus (Goldblatt et al., 1995; Manning & Goldblatt, 1996, 2005; Goldblatt & Manning, 1999, 2000), and *Watsonia* Mill. (Manning et al., 1999; Bernhardt & Goldblatt, 2006).

Pollination by hopliine beetles in *Babiana melanops*, *B. pygmaea*, *B. regia*, *B. rubrocyanea*, *B. stricta*, and *B. villosa* exploits the same set of floral characters described by Goldblatt et al. in southern Africa (1998b, 2000a, b) for *Aristea* Sol. in Aiton, *Ixia*, and *Sparaxis* and by Goldblatt and Bernhardt (1999) for *Moraea* Mill. The flowers of such species are exceptional in *Babiana* in being actinomorphic, usually having a comparatively short style, often darkly colored filaments, and anthers or pollen either brownish or violet to almost black; in *B. melanops*, *B. stricta*, and *B. villosa*, the flowers also have an expanded, dark-colored connective. The dark stamens or parts of stamens may contribute to the contrasting dark pigmentation common in beetle-pollinated species (Steiner, 1998; Goldblatt et al., 1998b, 2000b). Alternatively, unusually colored pollen may be a form of camouflage, as suggested by Goldblatt and Manning (1999), in which unconventionally colored pollen may not appear to be an edible resource for foraging female bees.

The situation in *Babiana melanops* is puzzling. One population at the southern extremity of its range has radially symmetric flowers with a floral odor and nectar and is visited actively by bee species, as well as hopliine scarabs (Table 3). Other populations have

odorless flowers that lack nectar and are visited exclusively by hopliines. An argument might be made for infraspecific status or even a separate species for the population, but other features of the population accord so closely with nectarless and odorless populations growing a short distance to the north that these alternatives have not been taken seriously. In some other predominantly hopliine-pollinated species, short-tongued bees or tabanid flies with probosces 4–5 mm long may occasionally be found visiting their flowers. Because hopliine flowers are salver-shaped or shallow bowl-shaped (sensu Faegri & van der Pijl, 1979), this is not surprising as the bright colors of the spreading tepals are readily seen and readily investigated by passing insects other than hopliines.

Pollination by night-flying moths and sunbirds is relatively unimportant in *Babiana*, and we infer that just six species have flowers adapted for these pollination systems, which appear to have evolved convergently, three times for moth pollination and twice for sunbird pollination (Table 5).

In summary, there are six discrete pollination systems in *Babiana*, a genus of only 90 species. Most of the species have a system using just one class of pollinator and, in the case of long-proboscid flies, usually just a single pollinator species. Species using two classes of pollinator are few and may either represent a transition from one system to another or have stabilized to exploit two different specialized systems. *Babiana stricta* is the most prominent example of a species with a mixed system; the spreading tepals of the radially symmetric perianth are often seen with resident hopliine beetles, while *Apis* and halictid bees are frequently observed foraging on the lightly scented flowers that offer

nectar as well as pollen rewards. The transition seems complete in the subspecies of *B. sambucina*, in which subsp. *sambucina* is consistently pollinated by bees and no population shows evidence of the shift to long-proboscid fly pollination characteristic of subsp. *longibracteata*. In *B. melanops*, different populations with small floral differences, whether scented and with nectar or not, permit different pollinator profiles, perhaps an example of a pollinator shift taking place today. The dynamics of these mixed systems are unknown, and shifts toward one or the other may track shifts in the prevalence of one or the other of the two groups of pollinators in response to changing environmental conditions.

FLORAL SYNDROMES AND SPECIALIST POLLINATION

In the debate concerning the importance of specialized versus generalist pollination and the utility of the floral syndrome concept (Waser, 1996), *Babiana* provides numerous examples of specialized flowers exhibiting discrete sets of floral traits (pollination syndromes). Hours of observation on various species with each set of traits repeatedly show the same result: a close link between floral presentation and pollinator class. In this genus, visits by what might be termed inappropriate visitors are rare, and few of them actually accomplish effective pollen transfer. The example of the long-proboscid *Prosoeca peringueyi* taking pollen from flowers of (apparently) large bee-pollinated *B. cedarbergensis* illustrates this dramatically. Several flies observed and captured while taking nectar failed to contact anthers and stigmas, and examination of the bodies of captured flies failed to show the presence of pollen of the species. *Babiana* provides one more example of a genus in a plant family in which pollination syndromes are highly predictive of the most effective (or only) pollinator and thus supports Johnson and Steiner's (2000) defense of the syndrome concept and the prevalence of specialist pollinator systems, at least in the tropics and the southern African temperate zone.

The fact that so many *Babiana* species depend on just one pollinator species is especially striking. Some 10 taxa are pollinated exclusively by *Prosoeca peringueyi* and three more only by *Prosoeca* sp. 1. Another four species are evidently pollinated only by *Moegistorhynchus longirostris*. These flies are clearly keystone species in the ecology of western southern Africa (Goldblatt et al., 1995; Goldblatt & Manning, 2000). Their extinction locally means one of two things: either failure to reproduce by seed (if self-incompatible or requiring mechanical pollen transfer even if self-compatible), or gradual inbreeding de-

pression for self-compatible and autogamous species. Not surprisingly, several such specialist species sometimes have fail-safe mechanisms and are facultatively autogamous. For the few long-proboscid fly-pollinated species for which compatibility relations are known, several show autogamy. *Lapeirousia jacquinii* and *L. oreogena* are prominent examples of such species in the *P. peringueyi* pollination guild (Goldblatt & Manning, 2000). *Babiana tubulosa* provides an example of facultative autogamy in the *M. longirostris* pollination guild, in which some other members (e.g., *L. anceps*) also exhibit this feature. Another species, the sunbird-pollinated *B. ringens*, is also self-compatible and shows a high self-pollination rate when access to pollinators is prevented (Anderson et al., 2005). We anticipate that further study of compatibility relations in species with few or single species pollinators will expand the list of facultative autogams in *Babiana*.

NECTAR VARIATION

Nectar chemical composition of *Babiana* species shows none of the variation in nectar sugar proportions sometimes correlated with differences in pollinators (e.g., Baker & Baker, 1983, 1990). Nectars are uniformly sucrose-dominant, and variation is largely in volume, with larger flowers with large-bodied pollinators producing greater amounts of nectar. Thus, sunbird-pollinated species produce the largest volumes of nectar, usually followed by long-proboscid fly-pollinated and moth-pollinated species. Beetle flowers produce little or no measurable nectar. Nectar concentration shows the same patterns observed in other genera of the Iridaceae (Bernhard & Goldblatt, 2006). Bee- and settling moth-pollinated flowers produce the most concentrated nectar, followed by long-proboscid fly-pollinated flowers. Bird-pollinated flowers often produce relatively dilute nectar (Goldblatt et al., 1999), and *Babiana* species in this category also show this trend. *Babiana* species pollinated by sunbirds do not show any evidence of the predicted trend toward the production of hexose-rich nectar found, for example, in a few species of bird-pollinated Iridaceae in the genera *Gladiolus*, *Klattia* Baker, *Witsenia* Thunb. (Goldblatt et al., 1999, 2001), *Chasmanthe* N. E. Br. (Goldblatt et al., 2004a), and *Tritoniopsis* (Manning & Goldblatt, 2005). Nectar sugar characteristics thus appear to be the result of phylogenetic history and are not pollinator driven, a conclusion consistent with patterns demonstrated, for example, by van Wyk et al. (1993) and Barnes et al. (1995) in some groups of Asphodelaceae and Ericaceae.

FREQUENCY OF POLLINATION SHIFTS

Passive pollen transfer by large-bodied bees appears ancestral in the genus, based on outgroup comparison (Davies et al., 2004; Goldblatt et al., 2006) and on its occurrence in the putatively least specialized species in the genus (Goldblatt & Manning, 2007). It is also inferred to be the primary pollination mechanism in some 58% of *Babiana* species, but we hypothesize that shifts to other strategies have occurred multiple times each (Table 5). Comparing the pollination system to our morphology-based classification of the genus (Goldblatt & Manning, 2007), we conclude that long-proboscid fly pollination, present in 20% of the species, arose independently four times. For exclusive hopliine beetle pollination, which is present in 7% of the genus, we infer a minimum of three shifts to this system. For pollination by pollen-collecting female bees, present in 6% of the genus, we infer two shifts, while moth pollination, present in three species, arose independently in each, and sunbird pollination, present in three species, arose twice. Therefore, because of the taxonomic distribution of derived pollination systems across the genus, we postulate that there have been multiple shifts of each of them and a minimum of 14 shifts in the genus, thus an average of one shift for every six species.

The diversity of pollination systems in *Babiana* mirrors that in other large genera of Iridaceae subfamily Crocoideae and is most comparable to the situation in *Gladiolus*. In that genus, there are 165 species in southern Africa and just one more pollination system (Goldblatt et al., 2001). Some 27 shifts in pollination system have been postulated for the genus in southern Africa, an average of one shift for every five species. Proportions of the different pollination systems differ marginally: long-proboscid fly pollination (18%); sunbird pollination (12%); moth pollination (7%); large butterfly pollination, which is absent in *Babiana* (5%); pollen-collecting bee pollination (2%); and beetle pollination (< 1%) of species. Clearly, hopliine beetle pollination has been exploited to a greater extent in *Babiana*, and both sunbird and moth pollination are proportionately less exploited. The proportions of long-proboscid fly pollination in the two genera are markedly similar, 18% in *Gladiolus* and 20% in *Babiana*.

PATTERNS OF STRUCTURAL CHANGE IN FLORAL MORPHOLOGY

A change in pollinator from an insect with relatively short mouthparts, such as apid bees, short-proboscid flies, and possibly other polyphagous taxa, to one with longer mouthparts, such as long-proboscid nemestri-

nids or sunbirds, may seem relatively insignificant. After all, this at first appears to be a moderate shift and one only of degree. It should, however, be remembered that a shift to a long-proboscid pollinator means a change from a system where several species of bee and fly, sometimes associated with hopliine beetles, may pollinate a species to one where only a single organism is the primary pollinator. Long-proboscid flies are particularly effective pollinators because there are relatively few species that offer them a reliable source of nectar and they usually carry heavy loads of pollen at specific parts of their bodies, limiting or excluding stigma clogging. The shorter-tongued insects, however, visit many species, sometimes in a non-constant pattern, and they usually carry mixed loads of pollen that are often randomly scattered over their bodies. These contrasting patterns of pollination must have important consequences for the reproductive systems of the two groups. One must conclude that a shift from a generalist to a specialist pollination system does have important consequences for the radiation of a genus, although the shift in morphological and physiological characters seems modest at best. Furthermore, *Babiana* remains the most compelling example yet among the genera of Iridaceae of an instance in which a distinct specialized pollination system, the *Prosoeca peringueyi* system, might have been stimulated to develop (Manning & Goldblatt, 1996).

The evolution of hopliine beetle pollination in *Babiana* involves perhaps the most complex set of morphological changes of any pollination shift. These include suppression of nectar production and associated reduction in the diameter of the perianth tube, loss of floral odor, change of perianth from zygomorphic with bilateral symmetry to actinomorphic with radial symmetry, the frequent development of bizarre color contrasts on the tepals, and, in some species of the genus, exaggerated size of the anthers, often combined with unconventional anther and pollen pigmentation. As in *Sparaxis* and *Tritonia*, genera of Iridaceae–Crocoideae that also have species with bilabiate zygomorphic flowers, as well as hopliine-pollinated species with radially symmetric perianths, these apparently unspecialized flowers are believed to be derived from ancestors with bilabiate flowers, and the change is believed to be directly associated with a shift to hopliine pollination (Goldblatt et al., 2000a). This flies against the conventional wisdom of floral evolution from a radial symmetry to zygomorphy with differentiation in size, shape, and orientation of the tepals. These observations suggest that a more dynamic view of floral evolution is required, where gross structural changes should be viewed against the adaptive background with which they are associated, and that outgroup comparison rather than degrees of

developmental complexity more reliably indicate the direction of change.

Lastly, we draw attention to comparisons of floral form and presentation with particular sets of pollinators in other genera of the Iridaceae, especially members of subfamily Crocoideae, where floral form is repeated again and again in different genera. As in *Gladiolus*, short-tubed, bilaterally symmetric gullet flowers, often of predominantly blue or sometimes pink color with pale nectar guides on the lower tepals and with strong floral odor, are pollinated by anthophorine bees and worker honeybees. Similarly colored flowers showing radial symmetry, scented or not, are pollinated by female bees foraging for pollen. Likewise, in *Lapeirousia*, long-tubed gullet or salver-shaped flowers with dark blue or purple pigmentation and pale nectar guides on the lower tepals, or with cream to pink flowers with reddish markings on the lower tepals, are pollinated by the same species of long-proboscid nemestrinid flies as we have expanded documentation in *Babiana*. In the same vein, pale-colored, scented flowers that are open at night show the same sets of moth pollinators as do species of *Hesperantha* and *Lapeirousia* with similar flowers. Red flowers pollinated by birds in *Babiana* show the same avian pollinators as do species of *Gladiolus* with similarly pigmented flowers with elongate perianth tubes that are wide in the upper half. These repeated trends in different genera allow us to predict with confidence the pollinators of species in other genera, the floral biology of which is incompletely known.

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